INDEX OF SUBJECTS.

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CORRIGENDA.

p. 18, line 16 from bottom, *for* and the *read* at this.

    „   bottom line, *for* fail *read* fails.

p. 54, line 4 from bottom, *for Prunus spinosa read Prunus lusi-*
    tanica, a planted tree, native in the Canary woods.

    „ line 2 from bottom, *for Sedum album read Sedum anglicum.*

p. 55, line 6 from bottom, *for Sedum album read Sedum anglicum.*

pp. 55, 57. headline *for* Lakes *read* Woods,

p. 57, bottom, *for* 1911 *read* 1912.

p. 277, *insert* The International Phytogeographical Excursion
     in the British Isles X *before title*.

p. 277, line 6 from bottom, *for* Lerregt *read* erregt, and *for* eitung
     read Leitung.

p. 283, footnote, first par., line 7 from bottom, *for* c. *read* c.

    „   „   second par., line 2 from bottom, *for* Masteich
     read Mastvieh.

RAY TRACHEIDS IN *SEQUOIA SEMPERVIRENS*.

BY MARJORIE GORDON.

[TEXT-FIGS. 1—7].

UNTIL recently it was thought that ray tracheids were absent from the genus *Sequoia*. Speaking of this genus Mayr in 1890 says: " die Markstrahlen bestehen durchaus aus Parenchym-zellen " (p. 271). In 1903, Jeffrey, in his special monograph on the Sequoias, makes no mention of ray tracheids. Gothan, in 1905, discovered ray tracheids in *S. gigantea*—" bei welcher species übrigens in altem Holz auch hier und da Quertracheiden vorkommen " (p. 848). Two years after Gothan's discovery, Penhallow, in the description of the genus in his text-book on the North American Gymnosperms (1907) states that the rays of the Sequoias are without tracheids (p. 223). Later, Jeffrey, in his article on *Cunninghamia sinensis* (1908) speaks of the finding of ray tracheids by Gothan in *S. gigantea* and adds that they " have not yet been found in *S. sempervirens* " (p. 598).

The material for this investigation was from a museum specimen of the wood of *S. sempervirens*. From its external features it could not be seen whether it came from near the pith or from the outer part of the stem. The microscopic character of the annual ring, however, shows it to have been from an old portion of a stem: the annual rings are flat, and there is very little indication of a " middle " layer—a feature in which, as Gothan has shown, old stem and root-wood often agree (see Fig. 7). In this wood both marginal and interspersed ray tracheids were found.

The marginal ray tracheids are different in shape from the central parenchymatous ray cells. Fig. 1 shows a radially elongated ray tracheid which extends along the ray for a distance equal to the width of two-and-a-half spring tracheids, is about half as high as a central cell, and has a very irregular free margin. Often these

cells are considerably shorter than the one figured. Fig. 2 shows a vertically elongated one. It also has a very irregular margin, but in radial extent covers only from one to one-and-a-half tracheids, while in vertical extent it is fully twice as high as the parenchyma cells of the ray. The height of the latter is quite uniform, and the cells have also very regular walls.

These elongated marginal ray tracheids recall some of the structures found in the pine by Thompson (1910, Fig. 13), which structures he considered of a primitive type ; and though in *Sequoia* no forms intermediate between the vertically elongated and the normal radially elongated ones were found, these vertically elongated structures are quite comparable to those of the pine, and are capable of a similar interpretation. Other marginal ray tracheids were found with sac-like projections from the end towards the cambium : these " tailed " ray tracheids have also their counterpart in the pine, chiefly in young root-wood, where Thompson states that the tails " seem to be due to an incomplete shortening of the tracheid as it turns along the ray " (p. 108), considered by him a vestigial feature in the process of ray tracheid formation from ordinary vertically arranged but short tracheary elements.
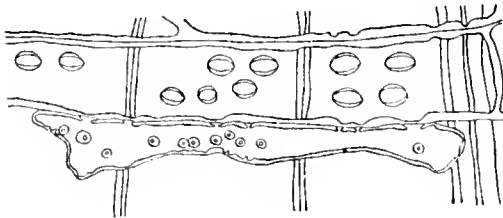
Fig. 1.
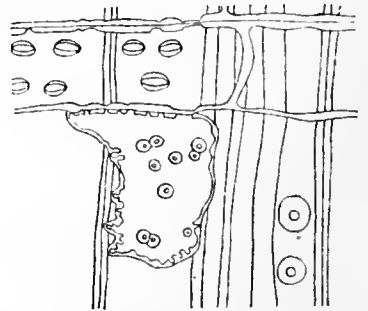
Fig. 2.

These various forms of ray tracheids occur on both sides of the medullary rays, not forming a definite row, but scattered along the rays. Sometimes they are found wholly in the spring wood (Fig. 3), but more often at the annual ring, the main part of the tracheid lying in the spring wood, but with a small part extending into the fall wood (Figs. 1 and 2).

The interspersed ray tracheids are similarly situated. Fig. 4 shows a radially elongated one. It extends over only one-and-a-half spring tracheids; but longer forms are quite common. Usually these cells are slightly less in height than the adjacent parenchyma cells (see Fig. 4). They are regular in outline, and although they closely resemble the ordinary ray cells in form, the pitting, as will be seen later, is very different. Fig. 5 shows two vertically

elongated ray tracheids. These vary in radial extent, are two to two-and-a-half times as high as the parenchymatous cells of the ray, and have irregular walls. They are similar to the "transitional" tracheids of the young root and young stem of the pines (Thompson, 1910, Fig. 11). They do not, however, as in the latter group, give rise to the normal ray tracheids if the rays between which they occur separate farther, whereas in the pine this has been shown to be an ordinary method of formation of marginal ray tracheids. Inasmuch, however, as they resemble in form and position these so-called "transitional" tracheids of the pines, they are of a primitive type.

There is thus in both marginal and interspersed ray tracheids of *S. sempervirens* much variability in form. Gothan (1905) has called attention to the variability in form of the ray tracheids in the other species of *Sequoia*, which he compares to those of *Picea* and *Larix*, but which he states are not so abnormal as those of *Thuja gigantea*, as figured by Mayr (1890). Gothan, however, did not figure those of *S. gigantea*.
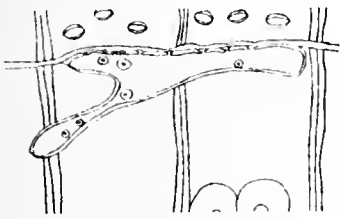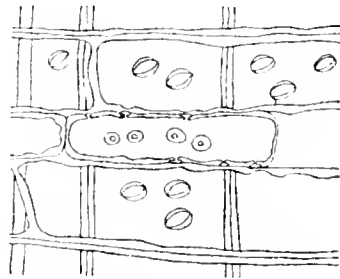
Fig. 3.   Fig. 4.

So far we have described the ray tracheids from the standpoint of size and form, and have noted certain differences in these features between them and the parenchyma cells. These features, however, do not give us sufficiently definite and accurate data by which to distinguish the two constituents of the ray, and in practice the pitting was made the criterion. It affords a ready and absolutely reliable basis. The radial pitting is especially serviceable, as seen in face view in the radial sections, which were found most adapted to this study. The pits thus seen (Figs. 1–3) are quite small but rather variable in size. Ordinarily they are not more than half the diameter of those where a tracheid touches a parenchymatous ray cell. These in turn are much smaller than the ordinary pits of the tracheids themselves (Figs. 2 and 3). In form, too, these three types of pits differ. The ordinary medullary ray cell pit is oval, and its border is confined to the upper and lower margins. This border

is not so broad in proportion to the size of the pit, as is that of
either the ray tracheid or of the ordinary tracheid. The borders of
the two latter also completely surround the pores. The pits on the
horizontal and terminal walls of the medullary ray cells are cut
across in the radial sections of the wood. The bordered (unilateral)
character of the pitting on the ray tracheid as it appears in section
where it touches a parenchyma cell finally distinguishes this element
from the simple pitted parenchyma cells of the ray. The appearance
of such pitting is indicated in most of the figures (see Fig. 1, etc.).
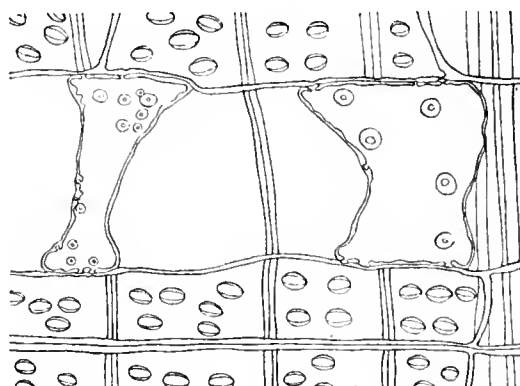
Fig. 5.
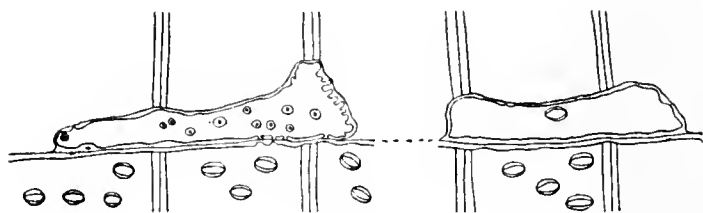
Fig. 6.

Text-Figs. 1—6   × 225.

In line with both marginal and interspersed ray tracheids
parenchyma cells are sometimes found—similarly shaped, and also
scattered, as are the ray tracheids. Fig. 4 shows an interspersed
ray tracheid which has to the left a parenchyma cell. Farther to
the left, beyond the figure, is a gap and then another ray tracheid.
Immediately to the right of the ray tracheid figured is a also gap,
after which there is another ray tracheid. Several series of inter-
spersed ray tracheids were followed towards the cambium and
invariably they disappeared and ultimately were not replaced by a
row of parenchyma cells, but the two parenchymatous portions of
the ray simply came closer together and " pinched out " the tracheary
elements. Figure 6 shows a marginal ray tracheid, which has a

parenchyma cell in line with it, a considerable distance to the left (the intervening portion has been omitted in the drawing). This condition was quite frequently observed. From the above description it will be seen that in *Sequoia* the replacement of ray tracheids by parenchyma is a very indefinite process, in contrast to the pines, nor do the cells follow one another continuously as in the latter group.

In the pines, where replacement is so definite, Professor Penhallow, and later Thompson, considered it indicative of transition between the elements, the latter clearly demonstrating that the tracheary element is the ancestral one. The indications in the transitional structures themselves are much better in *S. sempervirens* than in the pines, *simple* and *bordered* pits occurring on the *same element*. These are present on the horizontal walls (see Fig. 2): at the extreme left of the marginal cell is a bordered pit, then one with a less distinct border, and so on towards the right where there is an almost perfect simple pit, which is larger than any of the others. That the simple pits are really simple and not bordered is very clear, since the opening is the same width from top to bottom,
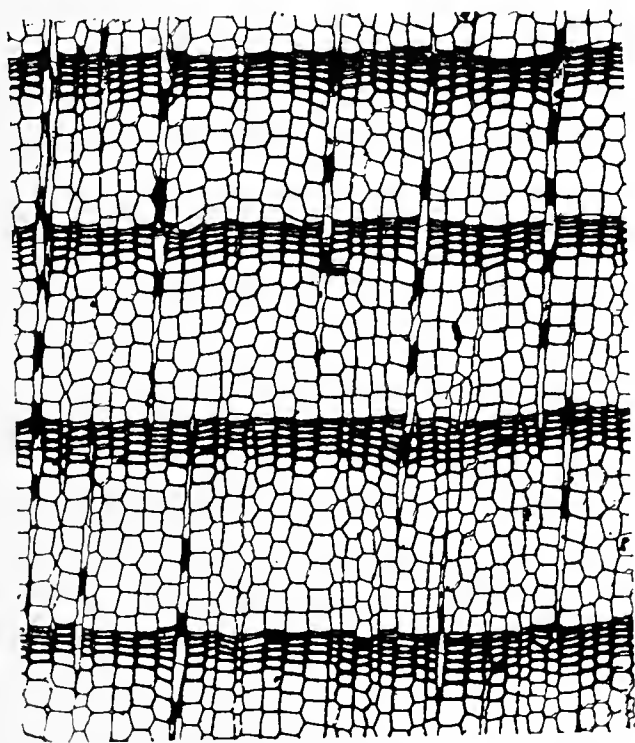
Fig, 7. Photograph of transverse section of the wood of *Sequoia semper-virens*, showing portions of four annual rings.　× 37·5.

or wider at the top, whereas a bordered pit, even if cut obliquely, would narrow towards the top. Mr. W. P. Thompson has found a similar feature in *Abies* (in press).

I have had access to fossil forms of *Sequoia* loaned by Director Brock of the Geological Survey at Ottawa, and also to a type set of *S. Penhallowii* presented to Mr. Thompson by Professor Jeffrey. No true ray tracheids were found. However, in *S. Penhallowii* Professor Jeffrey (1904) has noted that there are marginal cells which differ from the central cells in width, pitting, undulating borders, absence of tanniniferous contents, and presence of crystals (p. 327). Since the parenchymatous cells which replace the ray tracheids in *S. sempervirens* are quite different from the central cells in several of the features above mentioned, it is suggested that the marginal cells of *S. Penhallowii* may also be derivatives of ray tracheids.

The results of the present work have been to demonstrate the presence of ray tracheids, both marginal and interspersed, in old stem wood of *S. sempervirens*. This, in certain features of the structure of its annual ring, is comparable to root wood, and so of a primitive type. Gothan, to whom we owe our knowledge of this feature, compares such old stem wood of the pine to rootwood in another respect as well, the fewer resin canals which it contains, and so further suggests its primitive character. It is of interest that it is in this type of stem—which, though old, yet retains primitive features—that ray tracheids have been found ; and especially is it interesting since some of these ray tracheids are also of a primitive type. This feature makes it probable that when root wood is examined, or certain more primitive parts of the stem, ray tracheids will also be found. Since wounding appears to recall them in some forms (in *Cunninghamia*, Jeffrey, 1908, and *Abies*, Thompson, 1910) it would be interesting to know if such is the case here. No more material is available at present for further investigation, but it is thought desirable to publish these results at once, since the presence of ray tracheids in *S. sempervirens* has so recently been denied, and since the occurrence of the two kinds of pitting on the one element affords such a clear demonstration that there is a transition between ray tracheids and parenchyma.

It was on the suggestion of Mr. R. B. Thomson that this work was undertaken, and my heartiest thanks are due to him for his kindness and constant advice.

University of Toronto, 1911.

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POLYMORPHISM IN THE FLOWER OF *SILENE MARITIMA*.

By E. J. Salisbury, B.Sc., F.L.S.

(Quain Student in Botany, University College, London).

[With Plate I and a Text-Figure].

THE material used in the present paper was obtained in the summers of 1910 and 1911 whilst engaged as a member of Professor Oliver's ecological party in a study of the shingle beach flora at Blakeney Point in Norfolk. Here, as on nearly all pebble beaches, the Sea Campion (*Silene maritima*) is one of the most striking features of the vegetation, and it would probably be difficult to find a locality better suited to the study of this particular plant. At its distal extremity the main beach is, to a large extent, covered by sand dunes; and where the depth of sand is not great the Sea Campion is perhaps even more prevalent on this than on the shingle itself. The incursion of the typical sand dune plants soon, however, drive it out from the association.

Constantly coming before one's notice, the marked difference which the flowers exhibit is perhaps the most vivid impression that the plant presents. But here, and probably in many cases where there appears to be great structural range, further analysis shows

that the centre of variation is not single but multiple; even those forms which we do, after careful consideration, group together as continuous variations may, after all, be but an aggregate of strains, the differences between which are so small as to give the series an appearance of continuity. Recent research seems to point more and more to the external and visible differences as criteria of change established, relegating to the internal and invisible the steps which lead up to these mutations.

In the case under consideration there appear to be several well defined types around which variations of a lesser degree may be grouped. But in the absence of cultural experiments the conclusions can only be tentative: such evidence as is available, however, regarding their occurrence points strongly to the distinctness of the forms to be described.

a. outer, b. inner series
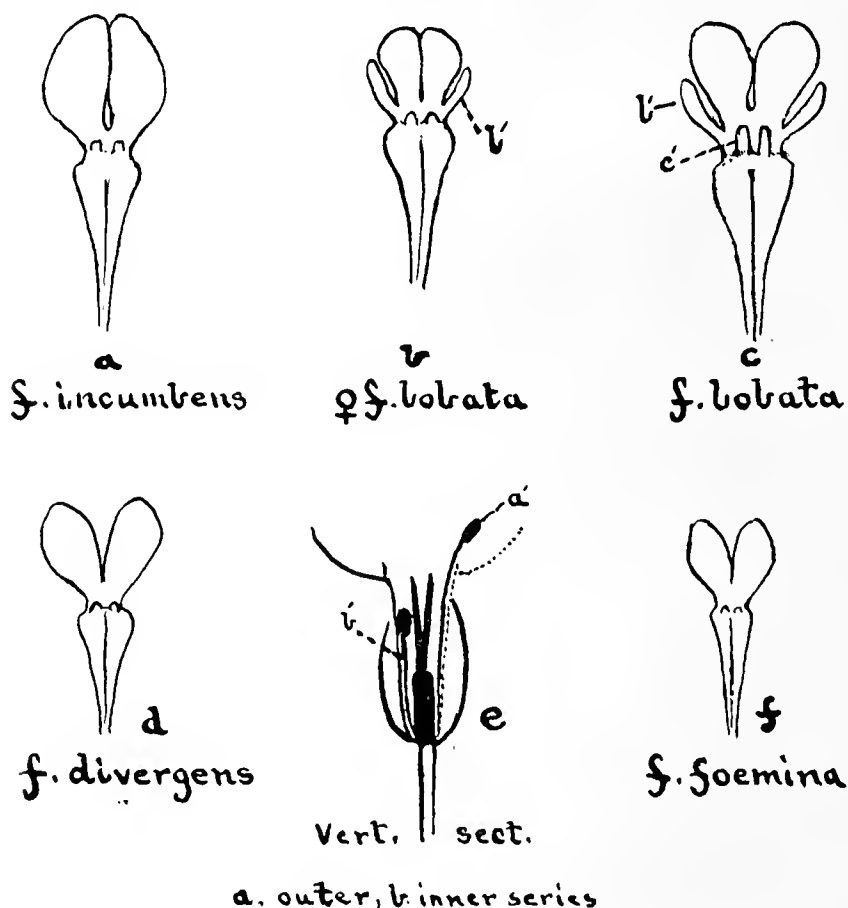
Text-figs. a to d and f, show spetals of some of the forms of *Silene maritima* represented as flattened into one plane. e, diagrammatic longitudinal section of an hermaphrodite flower in the phase when the outer series of stamens (a^1) are ripe and the inner series (b^1) are still in the corolla tube. c^1, coronal scale; l^1, lobelet.

In all cases observed the different types of flower occurred on different plants, often widely separated and frequently found as isolated specimens amongst other forms. All but three of the flower
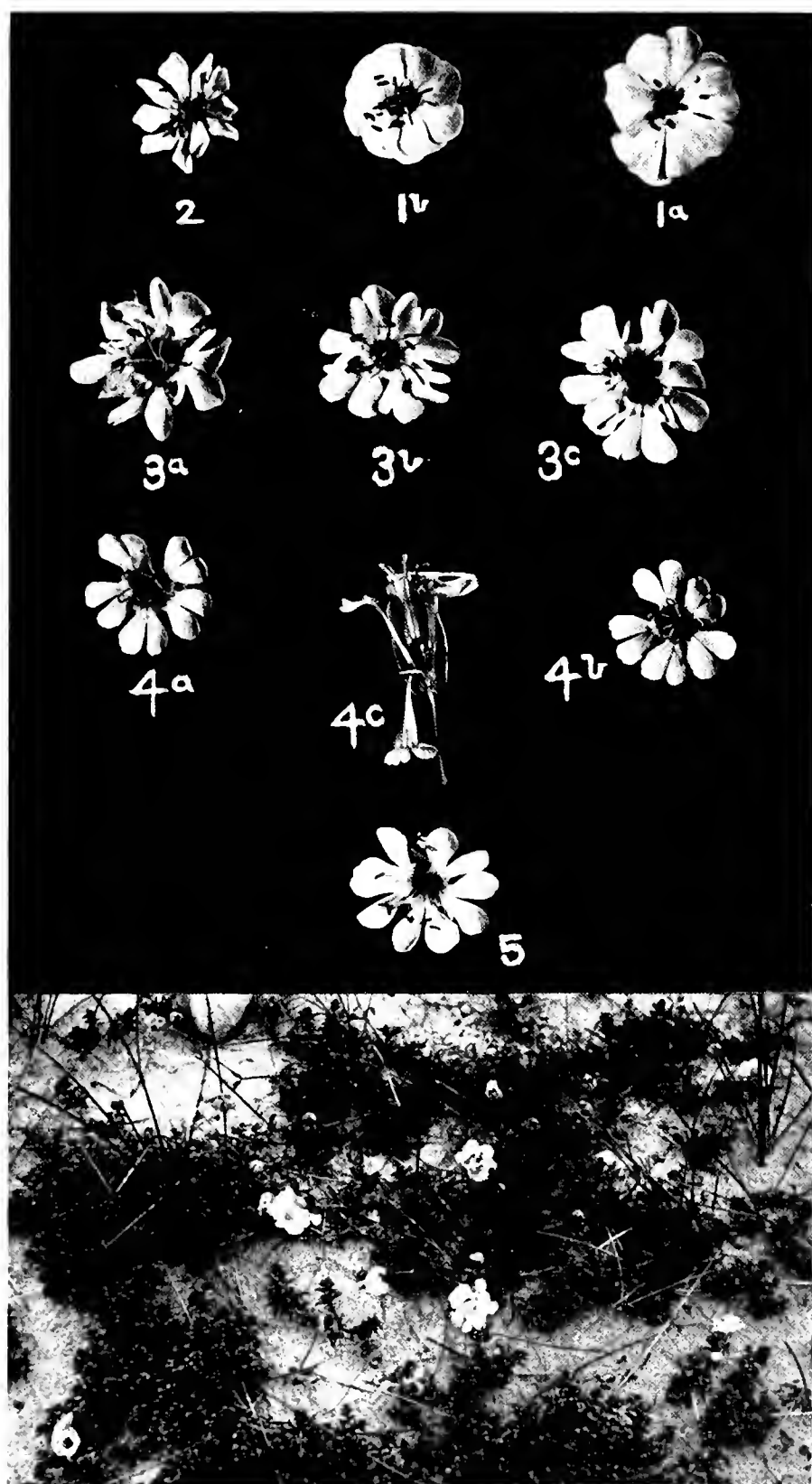
E.J.S. phot.

SALISBURY—*SILENE MARITIMA.*

types were also met with on the famous Chesil Bank in Dorset, thus indicating a wide distribution. In some of the forms to be described the sexual organs are incomplete, but in the four cases, where both stamens and stigmas are present, there is marked protandry. The sequence of development is as follows:—there are ten stamens in two whorls of five members each and of these the outer series elongate first and shed their pollen ; at this stage the second series may be seen with their anthers about half-way up the corolla tube (Text-fig., e). When this inner series has developed and dehisced the anthers of the outer series have usually either shrivelled, or fallen off the filaments. By the time all the anthers have shed their pollen the styles will have elongated beyond the corolla tube and their stigmatic surfaces diverged and curved backwards.

It may perhaps be well to mention that the unisexuality of some of the forms referred to above in which there are no functional stamens, have not been brought into this condition by the action of *Ustilago antherarum* ; this fungus is of very rare occurrence at Blakeney, so far having only been observed in one instance.

DESCRIPTION OF FORMS.

The commonest of all the forms has flowers from 20 to 25 mm. in diameter, and each of the five petals is divided into two lobes which either touch or slightly overlap in the median line (Text-fig. a). The contiguous petals also overlap and thus the flower at a short distance has the appearance of possessing a sympetalous corolla. Where the main portion of the petal joins on to the claw there is an abrupt waist-like narrowing and at this point two scale-like structures (the coronal scales) may be present, but are usually either small or entirely absent.

In Plate I, Fig. 1a, this form is shewn at the stage when the outer five stamens have dehisced and the inner series have appeared at the mouth of the corolla. Fig. 1b shews the same in a later stage ; the filaments of the outer series can be seen, but the anthers have dropped, the inner series have dehisced, and the stigmas are spread out for the reception of pollen from a flower in a younger stage of development. The points of variation are : the extent to which the petals are cleft ; the development of the coronal scales ; and the number of stigmas, which may vary from three to five.

Whilst fully recognising that the various types may themselves be aggregates of more closely allied forms it will be convenient both for description and reference, if we designate each by a name. The

form just described with its characteristic overlapping petals may thus be appropriately termed f. *incumbens.*

A second form which we shall call f. *divergens* approaches most closely to f. *incumbens*, and is nearly as frequent in its occurrence; also it has flowers of about the same size. The petals here are deeply divided and the two somewhat narrow lobes diverge from one another (Text-fig., d), whilst the outer margins of adjacent petals are either separate or only just overlap at the apex. Coronal scales are usually present, and the essential organs are normal. In the specimen figured (Plate I, fig. 5) one of the petals is slightly displaced so as to overlap the one adjacent.

Approaching rather closely to the last is another form, in which the lobes and petals diverge somewhat, but differing in the involution of both edges of each lobe, this extends from about half-way from the base to the apex. Owing to this character the lobes appear acute at the tip instead of rounded as is seen in Plate I., fig. 2. This form, which we will term f. *involuta*, is not of very frequent occurrence, its flowers are hermaphrodite and range in diameter from about 20 to 25 mm.

The last of the hermaphrodite forms is not very commonly found, but, of them all, it is perhaps the most beautiful. The flowers are not infrequently as much as 30 mm. in diameter, so that this form is the largest of any of the Sea Campions with the exception of a double form to be described later. Each petal is deeply divided, the two lobes diverging in the upper part; the petals as a whole also diverge very markedly from one another. The feature, however, which completely separates this from all but one of the other forms, is the presence of narrow lobelets arising symmetrically near the base of each lobe of the petal from its outer edge (Text-fig. b, c, l^1). These lobelets are narrow finger-like processes standing away from the major lobe and curving slightly towards the apex. They may attain a length of more than 5 mm. and usually curve slightly upwards from the general plane of the petal. The name f. *lobata* therefore seems to be most appropriate for this type.

Three flowers of this form are illustrated in figures 3a, 3b and 3c, where besides the characters already described the long coronal scales at the base of the petals are readily seen (especially in fig. 3c). The prominent development of these structures is a marked feature of this form which together with the upstanding lobelets give an almost double appearance to the flowers as seen in nature. There

are the normal number of stamens present and the stigmas vary, as is usual, from three to five.

A single plant was found at Cley with lateral lobelets as in f. *lobata*, but with somewhat smaller flowers (Text-fig. b): the stamens were all reduced to staminodes and the coronal scales were small. Whether this plant is more nearly related to f. *lobata* or to the next form is uncertain, but in the absence of corroborative specimens bearing this type of flower, a form name would be premature.

The next type, which will be best designated by the name f. *foemina* is very distinct both superficially and in detail. The flowers are much smaller than in any of the other forms, varying in diameter from about 10 to 15 mm., and are usually slightly purplish in colour. The petals are widely separated from one another and deeply cleft into divergent lobes which may bear at their base coronal scales (Text-fig. f); these are either very small or almost absent.

The most important feature of this plant is the unisexual character of its flowers which, as in the sub-form of f. *lobata*, possess no functional stamens, these organs having been reduced to staminodes. They are short, of about 5 to 6 mm. in length and bear very small abortive anthers at their apex. Plate I, figs. 4a, 4b, and 4c, illustrate three flowers : one of these (4c) has had part of the calyx and corolla removed to shew the staminodes which scarcely reach to the apex of the ovary.

The last type to be described has only been found at Blakeney Point, where three specimens now grow ; of these the first was found by Mr. R. J. Pinchin some years ago and two others in 1911.

All the essential organs have in this form become converted into petals and a considerable amount of " dédoublement " has taken place often resulting in a splitting of the calyx—a common feature in garden pinks which these flowers greatly resemble. In size the blooms vary from 30 to 40 mm. in diameter and are, if anything, slightly more cream-coloured than the single flowered forms. A plant growing in its natural habitat is shewn in Plate 1, fig. 6 with *Arenaria peploides* in the foreground.

The unisexuality met with in two of the types described may be regarded as a further advance upon the lines indicated by the marked protandry of the hermaphrodite forms. For whilst this mechanism ensures fertilisation by a different flower it does not of course preclude fertilisation by the pollen of a bloom on the same plant, as does the total suppression of functional male organs found in f. *foemina*.

Correlated with the differences in the flower there do not appear to be any constant corresponding differences in the vegetative organs.

The periods of flowering for the different forms have not been determined as this would require continual observation of the same area during some three to four months in the year. That they are of considerable duration may be gathered from the fact that all the seven forms were in flower at Blakeney during the first fortnight in July and four of these, viz., f. *incumbens ;* f. *divergens ;* f. *lobata* and f. *foemina*, were found at the Chesil Bank still bearing a few blooms as late as September 23rd. This much, however, can be said that from such observations as could be made some forms appear to differ in their period of maximum bloom ; f. *foemina* for instance seems to come into full flower slightly later than most of the other forms, whilst f. *incumbens*, and f. *divergens*, tend to flower early.

The following is a tabulation of these forms, together with their salient floral characters :—

Form.	Sex.	Characters.
f. *incumbens*	☿ ...	Petals overlapping.
f. *divergens*	☿ ...	Petals divergent.
f. *involuta*	☿ ...	Petals divergent and involute.
f. *lobata*	☿ ...	Petals with lateral lobelets.
f. *lobata*, female ...	♀ ...	Petals with lobelets. Androecium represented by staminodes.
f. *foemina*	♀ ...	Petals without lobelets, Androecium staminodal, fls., small.
f. *flore pleno*	O ...	Flowers double.

EXPLANATION OF PLATE 1.

Figs. 1a and 1b, f. *incumbens*. 1a, first series of anthers dehisced. 1b, second series of anthers dehisced, stigmas ripe. 2, f. *involuta*, stigmas not yet emerged. 3a—3c, f. *lobata*, shewing the lobelets and coronal scales. 4a—4c, f. *foemina*, shewing the diverging lobes and petals. 4c, calyx partially removed to shew the staminodes. 5, f. *divergens*. 6, plant of f. *florepleno* in its natural habitat, *Arenaria peploides* in the foreground and f. *foemina* on the right.

THEORIES OF THE ANATOMICAL TRANSITION FROM ROOT TO STEM.

By R. H. Compton.

[With a Figure in the Text].

THE varieties of national temperament exert on the advancement of Science an influence which may be beneficial or the reverse. Diversities of scientific outlook, methods and habits of thought when brought to bear upon a problem furnish a broad supply of material for generalisation. But, on the other hand, the mental distinctions of different nations, coinciding as they do with differences of language, produce a certain isolation which largely defies international synthesis : this is evinced by many an original paper or text-book, a perusal of which might lead to the conclusion that all the work worth mentioning had been done in the author's own country.

Nowhere is nationality more conspicuous than in the study of Plant-Anatomy. In Germany the subject is largely attacked from the physiological standpoint. In English-speaking countries the phylogenetic interest is paramount, and except where it bears on the new science of Ecology, physiological anatomy is somewhat neglected. In France and Belgium, however, we are largely without the physiological and phylogenetic aims, and anatomy is studied for its own sake, as in the early days of the science. France and Belgium are the homes of pure anatomy, and are rife with speculation and analysis to which we in England are a trifle indifferent, interested as we are rather in the applications of the facts to phylogeny. In Seedling Anatomy we continue to use the simple mode of description adopted by the early workers, and still speak of the Three Types of Transition according to Van Tieghem, to which Miss Sargant has added a Fourth Type whose importance appears to have been somewhat overestimated : and this although it has been long recognised in France that this method of envisaging the vascular transition does not adequately represent the facts. From our utilitarian phylogenetic point of view we are perhaps justified in adopting the simplest conventions possible : but this should not blind us to the fact that more recent analytical study has rendered these conventions obsolete as descriptions of the actual phenomena.

The recently published work of Chauveaud marks an important advance in the study of seedling anatomy—though not applicable to this part of the subject alone,—and it may perhaps be useful at

this stage to give a comparative account of the different aspects which the anatomical transition has borne in the eyes of certain prominent writers on the subject.

The early recognition of the stem and root as distinct morphological units, different in appearance, function, direction of growth, appendages, &c., directed attention to the region of the main axis where the change from root to stem is located. This region became known as the *collet*, a term to which the most diverse connotations were assigned. The early attempts at definition had regard only to external features, but in 1849 Clos introduced anatomical criteria into the discussion. It was only in 1858 that Naegeli pointed out the characteristic difference in the arrangement of the bundles of xylem and phloem in the stem and root of Dicotyledons. The work of Van Tieghem in 1871 gave a great incentive to the study of hypocotyl anatomy, and important papers, dealing with the transition phenomena of vascular plants, were published by Dodel, Mlle. Goldsmith and Gérard. The aim of the research was essentially the same in each case—to define the collet in terms of anatomy. Root and stem were regarded as by nature differently constructed, and the problem was to discover the device by which the two are put into connection. But though root and stem were regarded as objectively distinct, it was not doubted that the vascular strands are continuous throughout the whole axis. The transition [French ; *passage*] was conceived as a process of rearrangement, and the vascular strands were considered to contrive the connexion by means of splittings, rotations and fusions. No special interest attached to the transition structures, except a curiosity as to how the plant might tackle the awkward problem. The Three Types of Transition of Van Tieghem are merely descriptions of the manner in which this problem is solved in different cases. There is no need to discuss these Types in detail : the essential features of the

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DESCRIPTION OF FIGURES.

Diagrams of the transition from root-structure (below) to stem-structure (above) in Angiosperms according to various authors.

Column 1.   Gérard.   Black=xylem ; clear=phloem.

,,   2.   Sterckx. mc=median cotyledonary trace ; lc=lateral cotyledonary trace ; r=xylem pole of root.

,,   3.   Bonnier. xp=xylem pole ; pp=phloem pole.

,,   4.   Chauveaud. x=xylem ; p=phloem ; a=alternate ; i=intermediate ; s=superposed : 1, 2, 3 · · · =order of differentiation of vessels ; circles =vessels ; squares=sieve-tubes ; black= functional ; clear=degenerating.

Column 1. Column 2. Column 3. Column 4.
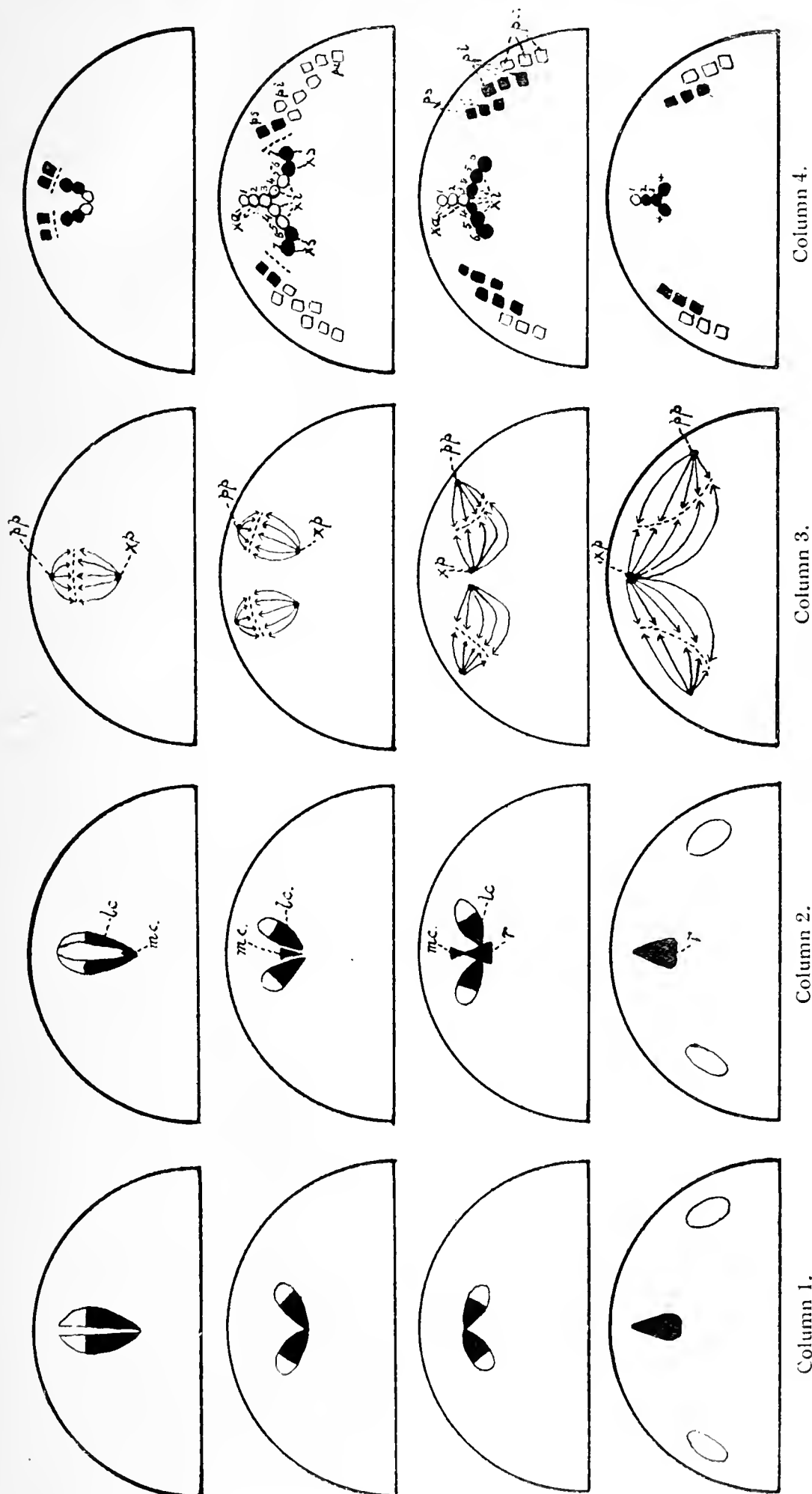
transition phenomena according to the earlier writers are sum-marised in column 1 of the figure which represents the Third Type. The xylem bundles remain in place, twisting through 180° as they ascend the axis; and the halves of the lateral phloems fuse radially outside the xylem. The chief merits of this view of the transition are that the vascular bundles are regarded as continuous from root to cotyledons, and that it furnishes a convenient method of description for comparative purposes. For this latter reason it has been almost universally adopted in England, despite many and obvious discrepancies with the facts of seedling structure. The most important fact ignored by this theory of Van Tieghem, Gérard, &c., is the common occurrence of a median protoxylem group between the main xylem bundles of the middle region of the transition. The error is not so serious in the simple case illustrated; but in a hypocotyl such as that of *Lupinus* spp., in which the lateral xylem bundles are widely separated from one another, the median proto-xylem cannot be overlooked. In such a case we are justified in speaking of the xylem bundles of the hypocotyl as forming triads, each consisting of a median polar " protoxylem " and a pair of lateral " metaxylems." Miss Thomas, while recognising the presence of the median protoxylem, yet speaks of the " double-bundle " as an anatomical unit : and the median and lateral xylems are regarded as constituting a single complex group. The work of Chauveaud throws much light on the nature of the median protoxylem, without, however, surmounting all the difficulties : and Miss Thomas' view can perhaps more easily be brought into accord with these than can the schemes of other writers. This subject must be considered later.

The views of Bonnier shew certain analogies with those of Gérard and Van Tieghem, and may be considered next. The scheme of transition according to Van Tieghem is not merely one of rotation : the position of the pole of xylem-differentiation changes relatively to the centre of the axis, the endodermis, &c. In the root the protoxylem lies towards the exterior of the central cylinder—a position of physiological value in relation to water absorption, according to Bonnier. As we ascend the axis the pole of xylem differentiation passes inwards, and is eventually separated from the pericycle by the whole thickness of primary xylem and phloem. Taking account of this gradual displacement by the xylem pole, Bonnier considered that the " central cylinder presents the same general plan of construction in both root and stem." He

expressed his view in a series of diagrams which may be sum-marised in column 3 of the figure. In the very young root rows of undifferentiated cells connect the first-formed xylem vessel with the first-formed phloem element. Along these files of cells differentiation proceeds simultaneously from phloem and xylem poles, as indicated by the arrows: the cells in between the last differentiated primary xylem and phloem elements remain meri-stematic and become cambium, represented by dotted lines in the diagram. The essential feature of the transition from root to stem, according to Bonnier's view, is the displacement inwards of the pole of xylem differentiation. This, acting concurrently with a relative approximation of the phloem poles and a separation of the xylem pole into two halves, is the chief cause of the different arrangements of vascular tissue in the seedling axis: the lines of differentiation always connect xylem and phloem poles like lines of force between opposite magnetic poles, and the points of first differentiation appear in moving to drag the lines of xylem and phloem initials with them.[1]

The views of Bonnier and Van Tieghem have much in common. Both ignore the median polar protoxylem of the hypocotyl: in this they are in contrast with the schemes of Sterckx and of Chauveaud. Both regard the conducting strands of the whole seedling as con-tinuous morphologically: in this they agree with Chauveaud, but stand in sharp opposition to the analytical ideas of Sterckx which we will now consider.[2]

The philosophical basis of the theory of Sterckx is the funda-mental distinctness of the morphological categories of leaf, stem and root. The plant is considered as capable of being cleanly dissected into the morphological units of which it is composed; the anatomy necessarily follows suit, and we have special leaf-traces, and special root-bundles. In the hypocotyl there is no confusion of structure; the respective traces of leaves, cotyledons and root are here *put into contact* with one another : there is no *passage* from root to stem structure, but only a juxtaposition of tissues for physiological convenience. The diagrams in column 2 of the figure, will shew how the transition is supposed to occur in

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[1] The uppermost figure is not given by Bonnier, who indeed says very little about the transition phenomena beyond what is implicit in his diagrams.

[2] Sterckx is selected as the representative of a school of thought since he has worked more particularly at seedling anatomy. Other names which must be mentioned are those of Gravis, Vuillemin and Dangeard. The diagrams in columns 1 and 2 are taken with some slight alterations from Sterckx's paper.

Nigella damascena which Sterckx chiefly studied. The cotyledon bundle is regarded as consisting of three parts, a median centrifugal and two laterals : into these parts it breaks up on entering the hypocotyl, and all three are inserted on a centripetal root-bundle. The cotyledonary trace dies away below, just as the root-bundle dies away above : there is a short region of *mise en rapport*, characterised, according to Sterckx, by the presence of specially short connecting vessels. " There is no continuation of the vessels of the root into the cotyledons, but there exist two sorts of wood elements; firstly those with centripetal development in the root and hypocotyl ; secondly those with centrifugal development in the cotyledonary node, cotyledons, stem and leaf." The analytical attitude of Sterckx is perhaps expressed most clearly by his criticism of the writers of whom Gérard is a type, who believe in the continuity of the vascular tissues of root, hypocotyl and cotyledons. " If the interpretation of these botanists were correct" says Sterckx " it would be necessary to admit that the cotyledons, contrary to other appendicular organs, have no insertion on the axis, that they have no bundles proper to themselves, and that their bundles are only the continuation of those of the root and hypocotyl : in other words, there would be no cotyledonary trace."

The recognition of a median and two lateral bundles constituting the cotyledonary trace is a step in advance of the views of Gérard and Bonnier, and of the theory of the *divergeant* of Bertrand and Cornaille adopted by Chodat. But many criticisms may be levelled and the interpretation of the facts. The view of Sterckx entails a rigid system of morphological categories from which, in a patchwork fashion, the plant is supposed to be compounded. Such a conception is impossible when the matter is considered phylogenetically. Morphological differentiation implies primitive homogeneity. This is so, whether we adopt the view that the leaf is an emergence from a primitively simple axis, or the view that leaf, stem and root alike arose by specialisation of an originally undifferentiated dichotomously branching thallus. The very existence of such an organ as the hypocotyl, which up to the present has resisted all efforts at classification, is sufficient to shew that the strict analytical morphology is insufficient, and that broader ideas based on comparative study and phylogeny can alone be satisfactory. The patchwork view of the vascular system — a system developed for the physiological purpose of linking differentiated plant-members—fail *à fortiori*.

The theories of seedling structure considered so far have little reference to the evolution of the vascular system. The study of stelar ontogeny in the Filicineæ has yielded rich phylogenetic inspiration: and it was expected that the seedling anatomy of Phanerogamæ would display primitive features which might cast light on the ancestry of the group. This expectation has not been realised in the same almost diagrammatic fashion as among Pteridophyta; but two main phylogenetic theories have emerged. In both of these there is no discussion of the stelar theory: it is the structure of the bundles which is under consideration.

Miss Thomas is responsible for the theory of the double bundle of which mention has already been made. Speaking of the simple diarch seedlings of the Ranales and Rhœadales she remarks "The striking feature in the cotyledon is the presence of a peculiar V-shaped bundle, which is obviously composed of two very definite halves, and has therefore been called a 'double bundle.' The apex of the V is occupied by a common group of protoxylem, while at the extremity of each arm is seated a phloem group." With this we may compare the conception of the "*divergeant*" of Bertrand and Cornaille: this anatomical unit is defined as "une masse libéro-ligneuse comprenant un groupe trachéen d'où partent deux lignes de différentiation ligneuse qui vont en s'écartant." The *divergeant* is a unit of great flexibility, and by means of a series of modifications—divisions, reductions, inflexions and so on—it is shewn that the vascular structures of the petioles of Ferns can be analysed into systems of *divergeants*: the whole being expressed in a curious shorthand notation. Miss Thomas' notion of the double bundle is almost equally fluid. "The double bundle," she says, "is sometimes represented by two quite separate bundles." And again, "*Cycas revoluta* may have its two central bundles replaced by a single one"—this also seeming to be the case in the "*Anemarrhena* type" of Miss Sargant. "The homology of the extreme forms is proved beyond question by the existence of a perfect series of intermediate cases . . . . . The function of these central bundles is always the same *viz.*, to form between them one pole of the root." It must be noted in passing that Miss Thomas' figures shew, what indeed is often very conspicuous, that the median protoxylem group is quite separate from the two lateral metaxylems with their superposed phloems: in fact the term "double bundle" is something of a misnomer, and "triple bundle" or 'more simply "triad" better expresses the facts in such cases. Though the presence of the

central detached protoxylem is recognised by Miss Thomas, she does not subscribe to the view of Sterckx that it is compounded partly of a median cotyledonary trace, partly of a root-pole. Her view rather approximates to the simple Gérardian conception of rotation of half-bundles about a protoxylem pivot, the isolation of the latter being regarded as unimportant. The special interest to Miss Thomas of the double bundle as an anatomical unit is not so much morphological as phylogenetic. She quotes a number of cases to demonstrate " the fairly universal presence of the double leaf-trace throughout the Fern-Gymnosperm series, and in a reduced form in the Angiosperms, together with its very frequent occurrence in modern Ferns." Its presence in Angiosperm cotyledons is held to be a primitive character, illustrative of the principle of onto-genetic recapitulation, and reminiscent of a fundamental dichotomous mode of branching. Such a phylogenetic theory marks a considerable advance on the merely descriptive and analytical views of earlier writers on the morphology of the vascular bundles of juvenile stages of development.

The second phylogenetic theory that has emerged from the study of spermophytic hypocotyls is due to Chauveaud, to whom we owe a series of papers during the last ten years, summarized and largely extended in an important work of 325 pages published in 1911.

Chauveaud promulgates a classification of vascular structures according to the relative positions of vessels and sieve-tubes. His view differs from the stelar theory of Van Teighem and numerous English and American authors, and from the theory of the *divergeant* of Bertrand, Cornaille and Chodat, in that both of these theories deal with tissues or groups of cells considered as plastic units, while Chauveaud treats of the direction of differentiation of the characteristic elements of which vascular tissues are composed— vessels and sieve-tubes—relatively to one another and to the symmetry of the plant-member. His is not a stelar-theory nor a bundle-theory, but a vascular-element-theory : it involves a closer and more particular—almost histological—study of tissues than do previous generalisations on vascular evolution, with the partial exception of the above-mentioned scheme of Bonnier.

Chauveaud's system is intended to apply to the whole of the vascular plants, but for our present purpose only three of his types need be considered. These are called respectively the alternate, the intermediate and the superposed. In the *" disposition alterne "*

the vessels are differentiated radially and centripetally, and groups of vessels alternate with groups of sieve-tubes round the circumference of the stele : this is the so-called " root-structure " and is represented in column 4 of the figure by vessels 1, 2 and 3, and by sieve-tubes labelled *pa*. The " *disposition intermediaire* " is that exhibited by the tangentially arranged vessels 4 and 5 and the sieve-tubes *pi*. and is intermediate between the alternate and the superposed arrangements. In the " *disposition superposée* " the vessels are differentiated radially and centrifugally, and lie on the same radius as the sieve-tubes : this is what is commonly known as " stem-structure," and is represented by vessels 6 and 7 and sieve-tubes *ps*.

These three types of arrangement are distinguished for the sake of convenience in description : actually they merge into one another. Chauveaud has shewn that in the ontogeny of certain parts of the Phanerogam axis these three phases of structure succeed one another in time—the alternate arrangement being the first to appear, this being followed by the intermediate and this again by the superposed : and he holds that this successive realisation in ontogeny is recapitulatory of vascular phylogeny. If we take sections of the base of the cotyledon of *Beta vulgaris*, for instance, in a very young state, we find two or three vessels and sieve-tubes in the alternate position. At a somewhat later stage more vascular elements are differentiated, these being situated in the intermediate position, the vessels forming a wing on each side of the alternate vessels, the latter being in the process of degeneration. At the fully developed stage a section through the same point shews both alternate and intermediate vessels re-absorbed, and the functional elements in the superposed position. This process is represented in the second diagram of column 4, those vessels and sieve tubes functional at the end of ontogeny being shewn black, the degenerate elements clear.

It may be noticed that the " *disposition superposée* " is capable of indefinite extension by means of the cambium. It is *par excellence* the position for continued growth, and as such it is adopted in the secondary thickening of plant members generally, root, stem and leaf.

This ontogenetic sequence of arrangements is found in a great number of Phanerogamic roots, hypocotyls and cotyledons, and also occurs in certain Cryptogamic stems. It is held by Chauveaud to be also a phylogenetic sequence. In the Angiosperm stem with the rarest exceptions the " *disposition superposée* " alone is realised :

this has its own "protoxylem" which is destroyed in the same way
as the "vaisseaux alternes" of the root, and corresponds to them
functionally, but belongs to a much later stage of evolution. This
is an example of what Chauveaud calls "l'accélération basifuge,"
by which, as we ascend the axis from root to stem we have early
stages of ontogeny successively omitted.

If we study a seedling by means of transverse sections taken,
not at successive times from the same place, but from different
places at the same time, we behold the changes in the disposition
of the tissues commonly known as the anatomical transition from
root to stem. According to Chauveaud the different structures
seen at different levels of the axis are all parts of his ideal scheme
of alternate, intermediate and superposed: the differences being
due to the fact that the initially formed elements belong to phases
of vascular evolution successively later as we ascend the axis. In
the root the first formed elements of the xylem are of the alternate
phase: half-way up the hypocotyl they may belong to the intermediate
phase, the alternate phase being unrepresented : at the summit of
the hypocotyl ontogeny may start with superposed protoxylem
elements, alternate and intermediate phases being omitted. Thus
the transition from root to stem is the expression of basifugal
acceleration. The protoxylem of the stem is not primitive in the
same sense as that of the root.

Chauveaud remarks that the sequence of phases is not strictly
adhered to in all cases : " the intermediate phase often seems to be
suppressed, and the passage from the alternate to the superposed
arrangement is abrupt. This is the case when the alternate vessels
meet one another at the centre ; when the xylem groups are very nu-
merous and closely approach the phloem groups ; or when the phloem
bundles, separated at first by alternate vessels, fuse with one another
after the suppression of these alternate vessels." To these exceptions
the present writer must add a case very pronounced in the large
seedlings of *Lupinus* spp., and of such frequent occurrence in other
plants as to become a normal and wide-spread type. In this type
the alternate and the superposed vessels are alone present in certain
regions of the hypocotyl, and are separated from one another by
greater or smaller distances: in *Lupinus hirsutus* as many as
fifteen parenchymatous cells may intervene on either side between
the median polar protoxylem and the two great collateral bundles
of common connection with it in the root. As we ascend from root
to hypocotyl the polar xylem has the appearance of forking into

these three groups, median and lateral, which may be fitly called a "triad": the "*disposition intermediaire*" is omitted at the higher levels and we pass directly from the alternate to the superposed phase—or in the older language from centripetal to centrifugal differentiation.

This frequent omission of the intermediate phase in the xylem is the chief weakness in the otherwise consistent and illuminating theory of recapitulation. It may be conceded that such "short-circuits" constantly occur in ontogeny, the organism forgetting (to use the mnemic metaphor) certain chapters of its evolutionary history. But in any case the "*phase intermediaire*" seems to be of quite subordinate importance in vascular phylogeny : it exists as an independent disposition only as an often fugitive stage in the transition from alternate to superposed arrangement ; and it apparently never forms the final term of an ontogenetic vascular series. In fact it appears to be mainly of physiological significance, no doubt serving as an aqueduct from the still functional "*vaisseaux alternes*" of the absorbing region of the axis to the "*vaisseaux superposés*" of its upper parts : and its frequent absence in situations where there is no such need (as in the case of triads) is consonant with a physiological rather than with a phylogenetic interpretation.

If we limit the number of phases to two, the alternate and the superposed, it is no new thesis that the former is primitive relatively to the latter. A long phylogenetic series from centripetal to centrifugal as the prevalent type of xylem has been outlined by Scott : and it may be remarked that *Poroxylon Edwardsii*, one of the members of Scott's phylogenetic series, is cited by Chauveaud as exhibiting his own three ontogenetic phases (though direct evidence is lacking here). The demonstration that the theoretical phylogenetic sequence is realised in the ontogeny of the hypocotyledonary axis of Phanerogams, together with the notion of basifugal acceleration, are the most noteworthy original generalisations in Chauveaud's work.

The theory of the nature of the anatomical transition from root to stem proposed by Chauveaud differs from others previously considered by reason of its phylogenetic content. The obvious affinity with Bonnier's scheme is only superficial : for according to Bonnier we have a gradual repulsion of protoxylems from the periphery towards the centre of the stele as we ascend the hypocotyledonary axis ; while according to Chauveaud the protoxylem of the "*disposition superposée*" belongs to a later phase of vascular

evolution than that of the "*disposition alterne.*" For similar reasons Chauveaud's theory differs from Gérard's "triple hypothesis of identity (of vascular strands as between root and stem), doubling and rotation": and the same applies to any theory based on the *divergeant* as an anatomical unit. Further it is clearly incompatible with the "contact" theory of Sterckx. Its relation to Miss Thomas' theory of the double bundle and dichotomy is of interest· The different types of double bundle and the "perfect series of intermediate cases" are brought into relation with one another as different phases of an evolutionary cycle which the vascular strands may pass through, both in time at one and the same level, and in space (as we ascend the hypocotyledonary axis) at one and the same time. The tendency of Chauveaud's work is to indicate that appearances of doubleness in the vascular strands of cotyledons are related to their direct connection with the "*disposition alterne*" of the root; and this runs counter to Miss Thomas' view that they are reminiscent of ancestral dichotomy.

The greater part of Chauveaud's detailed work is directed to establishing the series of phases of structure, and is carried out by means of sections of the same part of the seedling at different stages of development. The ordinary investigation of the transition phenomena is carried out by means of sections of different parts of the seedling at the same stage of development. Both methods of study are legitimate and useful, and the validity of the latter is unaffected by Chauveaud's demonstrations, which, however, throw a flood of light on the processes observed.

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THE INTERNATIONAL PHYTOGEOGRAPHICAL EXCURSION IN THE BRITISH ISLES.

IV.—IMPRESSIONS OF THE FOREIGN MEMBERS OF THE PARTY.

1.—PROFESSOR H. C. COWLES.

IT is too early to determine the most striking results of this excursion to the science of Photogeography, but it is not too early to predict with certainty that its influence will be very important and far-reaching. It is easier to distinguish the benefits of the excursion to its participants than to the science in general. I have felt that the chief benefit to me has been the opportunity of living for a month in intimate relationship with my phytogeographic colleagues of other countries, of knowing them from many points of view, and thus of coming to feel that they are friends, as well as fellow scientists. This month of living and travelling together

made us much better acquainted with each other's views and field interpretations, and also made it possible to read each other's writings much more understandingly than heretofore. Close companionship has made us more sympathetic with opposing view-points, and more ready to see at least some truth in views we thought were wholly wrong. Such results must come from every excursion of this sort, and if only we have enough of them to bring all the active phytogeographers of the world into sympathetic touch with others of their kind, we may hope soon to see a marked diminution in the misunderstanding of view-points, and in the amount of polemic literature. It is from such intimate acquaintance-ship among the workers and, perhaps, only thus that we may hope for constructive advances in securing uniformity of terms and methods. For example, it is difficult for an American to understand from the literature the precise signification of such terms as heath or moor, but in the field last summer these and other terms of the European workers were so often illustrated by concrete examples that they became thoroughly familiar.

As an American, I was, of course, much interested in seeing intelligently new kinds of vegetation. To the European members of the party this joy was much less possible, although there seemed to be points of considerable variance, even with Continental Europe. I was amazed at the vast amount of wild country in densely populated England. The extensive areas of the Broads, the sand-dunes and salt-marshes, the numerous heaths and moorlands, were more widespread and much more natural than I had expected them to be. While America may be more fortunate than Europe in the possession of great natural formations of plants, I was fully con-vinced that in the British Isles, at least, there is quite enough to occupy phytogeographic students actively for a long time to come. Many successional series were observed, whose progression or retrogression was quite as evident as in American formations, and to whose significance the British workers are fully alive.

I cannot close these rambling notes without expressing my admiration for the splendid organization of the British plant geographers. Doubtless it is largely this that has enabled them to accomplish so much in so short a time. My admiration for British social customs, as we saw them, is also very great. The hearty greetings that met us everywhere, the interest expressed in our work on the part even of those who could know little of it, the constant display of whole-souled British hospitality—all these things and many more have made August, 1911, a most memorable period in our lives.

HENRY C. COWLES.

The University of Chicago.

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2.—PROFESSOR JEAN MASSART.

Les points qui m'ont frappé le plus vivement pendant l'excursion sont les suivants.

1. L'abondance et la beauté des grands arbres, surtout des chênes, qui vivent partout entre les champs et au bord des chemins.

2. La douceur extraordinaire du climat, permettant de cultiver en plein air : (a) à Cambridge, *Encalyptus Gunnii, Viburnum Tinus, Quercus Ilex* ; (b) presque dans les Highlands *Araucaria excelsa, Tropæolum speciosum* ; (c) en Irlande *Passiflora cærulea, Bambusa fastuosa, Musa Bajoo, Cordyline australis* ; (d) en Cornouaille, des fougères arborescentes (*Dicksonia antarctica*).

C'est surtout en Irlande et en Cornouaille que le caractère maritime du climat est accentué : *Arbutus Unedo, Potentilla fruticosa, Erica vagans, E. ciliaris.* Les fougères et les *Saxifraga* vivent en épiphytes à Killarney.

3. La présence d' espèces alpines et subalpines au niveau de la plaine : (a) *Selaginella spinulosa, Pinguicula vulgaris, Primula farinosa*, à Haweswater Lake (en Silverdale, Lancashire du nord) ; (b) *Dryas octopetala, Arctostaphylos alpina, Empetrum nigrum*, à Ballyvaghan (en Irlande de l'ouest).

4. L'étendue des espaces qui sont laissés incultes pour le gibier, et qui sont couverts, soit de *Pteridium aquilinum, Nardus stricta*, etc., soit de tourbières sèches avec *Eriophorum vaginatum, Rubus Chamæmorus, Empetrum nigrum*, etc.

5. La présence d'anciennes forêts dans ces tourbières.

6. La grande extension de *Rhacomitrium lanuginosum* sur les montagnes (Cross Fell et Ben Lawers), et les touffes, curieusement modelées par le vent, de cette même mousse sur le plateau de Cross Fell.

7. Les plantes aquatiques submergées de la Cam, à Cambridge : *Scirpus lacustris, Sagittaria sagittifolia, Œnanthe fluviatilis.*

8. Dans les Norfolk Broads : (a) l'envahissement de l'eau par les plantes aquatiques, et la création de prairies branlantes ; (b) les " carrs " où la végétation est vierge de toute intervention humaine.

9. La rencontre, à Blakeney Point, en Norfolk, d'espèces meridionales (*Suæda fruticosa, Frankenia pulverulenta*) et d'espèces septentrionales (*Mertensia maritima*).

10. Dans les dunes de Southport, la similitude de la flore des collines de sable et des pannes, avec celle des dunes littorales de Belgique.

11. La variété de la flore alpine de Ben Lawers.

12. La présence de bois de *Taxus* sur le calcaire (Silverdale, Lancashire du nord) et sur la craie (près de Chichester).

13. L'abondance de plantes calcifuges sur le calcaire en Silverdale et à Ballyvaghan, notamment *Pteridium* et *Calluna*.

14. *Last not least*, l'amabilité et la grande compétence des botanistes anglais, qui nous ont permis de voir enormément de choses en un mois.

<div align="right">J. MASSART.</div>

Université de Bruxelles.

3.—PROFESSOR C. A. M. LINDMAN.

My Dear Tansley,

In a recent number of The New Phytologist you gave a full account of the International Phytogeographical Excursion in the British Isles of this year. This forms very pleasant reading for the foreign members of the party. Your description will give them a solid and instructive *souvenir* of this interesting tour,

As one of the foreign botanists I beg you to allow me to express in your Journal some general impressions of the " I.P.E." in 1911.

The vegetation of your country has only one defect, a defect that is shared by our own : they are both out of the way, neither country lies on any great European route, and so they are not well known to the botanists of the Continent. For instance, the Royal Botanic Museum at Stockholm—well filled with collections from most countries, brought home by keen Swedish floristic botanists and travellers—still lacks herbarium specimens from the British Isles, except a few sheets sent by J. E. Smith, and, in later times by the brothers Linton and Groves. A more frequent intercourse across the North Sea would be useful to contribute to the understanding of various floristic and phytogeographical questions, and to clear up several confusions. No doubt then a properly organized trip through the British Isles must be a first-class event in European phytogeography and a great attraction to any foreign naturalist. So I found it, and I can truly say that I saw and learned much more during the excursion than I ever expected. And I gladly testify, on my own behalf, and on behalf of my colleagues, that however much we had seen in different countries, we still found many peculiarities in the British vegetation, which are not to be seen elsewhere, and many features, which are as striking and interesting as any we have ever met with.

This, I think, may be said of the objects of the very first excursions, the vast fens, carrs and broads of Norfolk; and the same is true of the lonely moors and hill pastures of the Pennines, the shingle banks along the sea-shores, the great chalk-slopes of Kingley Vale in Sussex, with their wonderful yew woods, the dripping sub-tropical fern-clefts of Killarney, and the remarkable plains of Galway and of Cornwall, where the singular scenery is emphasised by the strange peculiarities of the flora.

Indeed, if only a part of this abundance had been offered to us we might have felt quite satisfied and surprised. But, by the skilful organisation of the British Vegetation Committee, and by the aid of many other persons and institutions, we were easily able to see the most interesting things and the most beautiful scenery in Great Britain and Ireland, that botanists would want to know. And we all assuredly recognized that the whole excursion was arranged *crescendo*, continually passing to more interesting subjects, more pregnant plant formations, and more striking scenery. Hence the lustre of your " I.P.E.," heightened by the experience of the never failing sunshine of the brightest British summer in the memory of man.

My own observations are perhaps but little important, but I made a good many, both ecological and floristic. I shall not, however, mention them to-day. I will only add that I appreciated very much the many occasions of getting acquainted with British botanists and of seeing them at their work. I am also indebted to you all for much kindness and courtesy.

C. A. M. LINDMAN,
Director of the Royal Botanic Museum.

STOCKHOLM,
December, 1911.

NOTES ON RECENT LITERATURE.

PALÆOBOTANY.

MORPHOLOGICAL FEATURES IN THE PALÆOZOIC FERN *Psaronius.*

"Die Tiefschwarze *Psaronius Haidingeri* von Manebach in Thüringen." By H. Graf zu Solms-Laubach. *Zeitschrift für Botanik*, 3 Jahrgang, 1911, Heft II., p. 721.

THE petrified tree-fern stems which Cotta named *Psaronius* nearly eighty years ago have long attracted the attention of collectors and students of ancient plants. One of the results of the discovery that many of the supposed fern fronds preserved in Palæozoic strata were borne by seed-bearing plants and not by true ferns is that such relatively few Carboniferous plants as are still accepted as ferns have gained in importance, and any fresh light on their structure and affinities is therefore particularly welcome. The various species of *Psaronius* are generally admitted to show a closer affinity with the recent Marattiaceæ than with any other group of Filicales. The admirable investigations of Professor Zeiller have contributed more than those of any other author to our knowledge of the anatomy of this genus, though there are still several points on which further information is needed. The central region of *Psaronius* is occupied by a system of concentrically disposed vascular steles which in transverse section present the appearance of flat or curved bands of xylem surrounded by a narrow zone of phloem. These vascular strands are embedded in parenchymatous tissue in which sclerenchyma is present either as a band enclosing the central stelar region or in the form of plates in close association with the more peripheral vascular tissue. External to the mechanical tissue the stem is surrounded by a broad parenchymatous envelope enclosing numerous roots which pursue a more or less sinuous course parallel to the axis of the stem. Beyond this tissue with its accompanying roots some stems possess a felted mass of external roots without any enveloping parenchyma. It was to the elucidation of the nature of the parenchymatous zone with roots that the researches of Count Solms were primarily directed.

The natural interpretation of the outer zone of a *Psaronius* stem would be to regard it as cortical tissue penetrated by adventitious roots, as in the stems of Marattiaceæ. It has been shown by Stenzel and other authors that there are difficulties in the way of this interpretation. Leaf-traces are not found in the root-bearing zone nor can old leaf-scars be recognised on the external surface of the stem. These and other considerations led Stenzel to express the opinion that " the cortical zone formed a narrow band in the young leaf-covered stem "; and that " after leaf-fall it became the seat of active growth in its inner layers and so produced a constantly widening zone of secondary parenchyma, which pushed the superficial cortical tissue with the leaf-bases or leaf-scars further out until it was exfoliated." [1] This view has been accepted, though not always without hesitation, by several writers. Farmer and Hill in their paper " On the Arrangement and Structure of the Vasrcula

[1] Seward, " Fossil Plants," vol. II, p. 417, 1910.

Strands in *Angiopteris evecta*, and some other Marattiaceæ,"[1] recognise the difficulty of accepting Stenzel's explanation of the nature of the root-bearing region and draw attention to certain important differences between *Psaronius* stems and those of recent Marattiaceæ. The root in the Marattiaceous cortex, as these authors point out, " is obviously an intrusive organ. But in *Psaronius*, in the best preserved sections that we have seen, the outer cortex surrounding the zone of small-celled sclerenchyma, and forming a peripheral ring in the roots, passes almost insensibly into the parenchymatous tissue between them. Furthermore, the cells of the latter are very irregular in character, often producing the effect of elongated cells ' combed' in various directions."[2] Count Solms discusses with his usual thoroughness the nature of the root-zone, and as the result of an examination of several species of *Psaronius* he adduces important evidence confirming the doubts expressed by Farmer and Hill. The roots which lie clear of the stem occasionally show distinct indications of cell-division and growth in their cortical tissue. This is clearly demonstrated by a transverse section of a root figured by Solms in which the cortex has a very irregular contour and on one side has grown out into a projecting wing of parenchyma consisting of radially disposed rows of cells. The inner roots are embedded in parenchymatous tissue which Stenzel speaks of as stem cortex, and Solms, adopting Rudolph's term, designates filling tissue (Füllgewebe). This tissue consists of rows of elongated cells radiating outwards from the edge of the stem cortex: these rows are usually in contact with the sclerenchymatous margin of the slightly flattened roots, while at the narrower edges of the roots the rows of elongated cells pass directly into the sclerenchymatous cortex with which they are in organic connection. This radially extended tissue forms longer or shorter tongue-like layers of cells which have been developed by the growth and elongation of the outer cortex of the roots. In the accompanying figure reproduced from the paper by Solms, I and O denote respectively the inner and outer part of the stem in their relation to the roots. The relation between roots and enclosing parenchyma is strikingly different from that between the roots of Marattiaceæ and the cortex penetrated by them : in the latter each root is surrounded by crushed cells of the stem cortex. In the *Psaronius* roots, on the other hand, the parenchyma owes its origin to the outgrowth of groups of filamentous hairs which eventually form a continuous mass of parenchyma. When the filling-tissue abuts on the side of a root facing the centre of the stem (*a*, in the figure) its cells curve right and left and apply themselves to the outside of the sclerenchymatous zone. It would seem, therefore, that on the side near the centre of the stem this parenchymatous tissue becomes concrescent with the root cortex, while on the opposite side there was an active growth and prolongation of the superficial cells of the root cortex.

It is difficult as a rule to recognise the original stem cortex to which the proximal ends of the roots were attached, but Solms figures a portion of a transverse section of a root surrounded

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[1] Annals of Botany, vol. XVI, p. 371, 1902.

[2] *Ibid*, p. 382.

by the ground-tissue of the stem from which it is sharply delimited, a relation between root and stem in marked contrast to that between the roots and the filling tissue in the extra-cortical region.

The conclusions reached may be summarised as follows :— The *Psaronius* stem has a thin cortex bounded by a fairly thick hypodermal band of mechanical tissue. This cortical region is penetrated by adventitious roots which arise in the internal tissues of the stem. Hair-like outgrowths composed of cell-rows are developed from the epidermis of the stem and these eventually form

I

O
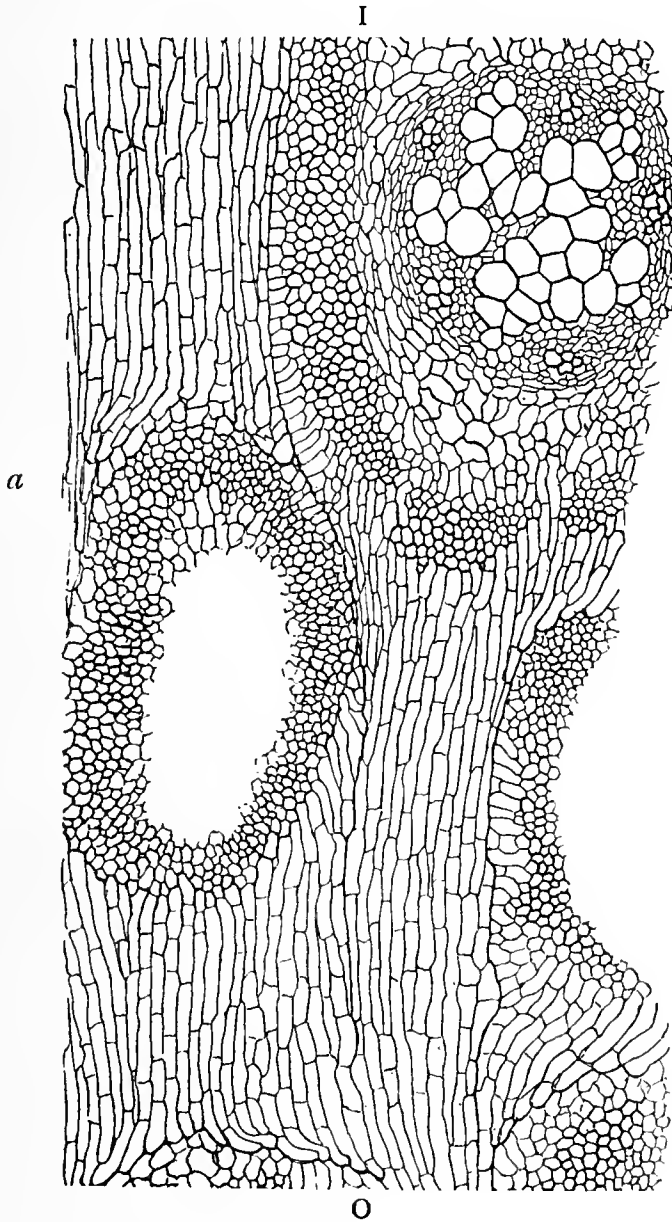
Psaronius sp. Transverse section of part of the root—enclosing parenchyma. I, O, inner and outer side of the section ; *a*, concrescence of filling-tissue with the sclerenchyma of a root. (From Solms-Laubach's specimen in the Rio Janeiro Museum, Coll. Solms, No. 592).

part of the root-enclosing parenchyma. The roots after emerging from the cortex pursue a downward course along the stem surface; they grow between the hairs of the filling-tissue and their inner flanks become concrescent with the outgrowing hairy tissue

(produced from the stem) which abuts on them. This union of two distinct tissues is a feature difficult to understand. As the growth of the stem proceeds, additional roots are developed and these grow over the older roots. The latter have meanwhile produced outward extensions of their cortex differing only in their root-origin from those previously developed from the surface of the stem, and this tissue becomes intimately connected with the inner flanks of the later-formed roots. The parenchymatous tissue external to the original stem is thus formed in part by the outward extension of the stem cortex and in part by the development of the same type of tissue from the cortex of the roots. Instead of root hairs of the ordinary type, the roots of *Psaronius* produced multicellular outgrowths in which they became enveloped as in a cortex, a phenomenon to which living ferns have so far afforded no parallel.

In addition to the new evidence obtained in regard to the nature of the extra-stelar tissues of *Psaronius*, Count Solms deals also with some other questions of morphological interest. One of these is the supposed secondary thickening described in 1899 by Butterworth[1] in the root of *Psaronius Cromptonensis*. A brief description is given of a root of *P. Weberi* from Chemnitz in which a fan-shaped group of tracheæ is attached to the end of one of the stelar arms. These divergent series of xylem elements are considered to be connected with the origin of a lateral root and to correspond with the "pédicule" of van Teighem. In other roots examined similar supernumerary groups of tracheæ were noticed in contact with more than one arm of the stele. It is suggested that the supposed secondary xylem of Butterworth may consist of several such groups, and if this is the case, it means that in *P. Cromptonensis* all the xylem arms of the root were implicated in the origin of the vascular supply of a lateral root. Incidentally it is pointee out that in *Angiopteris* several xylem strands of a root stele ard concerned in the production of the xylem of a lateral root, whereas in recent ferns generally, only one arm of the xylem is affected by the development of a lateral root, a fact of some importance in regard to the systematic position of the Palæozoic genus.

Though there is little doubt as to a close affinity between *Psaronius* and recent Marattiaceæ, the work of Count Solms may be considered to lend support to the retention of the family-name Psaronieæ, instead of the inclusion of the genus in Marattiaceæ.

In the current number of the *Berichte*[2] of the German Botanical Society, Julius Schuster publishes a note, with illustrations, on a fern-stem recently described by Professor Pohlig as *Xylopsaronius Cottai* (Corda). This generic name was given by Pohlig to Corda's Permian species from Hilbersdorf, near Chemnitz, on the ground that the stem possessed secondary wood. An examination of sections cut from the original block demonstrated that the supposed secondary xylem consists of regular series of parenchymatous cells extending in a radial direction between the numerous adventitious roots, and affords a typical

[1] Manchester Lit. Phil. Soc., Mem. & Proc., 1898-99, Vol. 43, 1900.
[2] Xylopsaronius ., . der erste Farn mit sekundärem Holz ? *Berichte der deutschen Botanischen Geselleschaft*, Bd. XXIX, *Heft* 8, p. 545, 1911.

example of the filling-tissue described by Count Solms. A comparison of the figures given by Schuster with those in Solms' paper leaves no doubt as to the correctness of this conclusion.

<div align="right">A.C.S.</div>

The Glossopteris Flora.

"On the Geological Structure and History of the Falkland Islands." By T. G. Halle. (Reprinted from the *Bull. Geol. Instit. Univ. Upsala*, Vol. XI., p. 115, 1911). " Les phénomènes glaciaires de l'époque Permo-Carbonifère : indications climatériques fournies par le flore." By P. Bertrand. (*Ann. soc. geol. du Nord*, Vol. XXXVIII., p. 92, Lille, 1909).

ALTHOUGH the title of Dr. Halle's memoir does not afford any indication of the fact, some of his results are of considerable botanical interest. He describes certain fossil plants which demonstrate the existence of the *Glossopteris* flora in the Falkland Islands, and in association with the plant-beds he discovered rocks of undoubted glacial origin. The term Glossopteris flora, first used by Neumayr in 1887, is applied to an assemblage of Palæozoic plants from India and the southern hemisphere characterised by a comparatively small number of species, by a wide geographical distribution, and by a general uniformity of facies. Our knowledge of the nature of the individual members of the flora is very meagre as it is based almost entirely on casts and impressions of leaves and stems, but from the point of view of distribution and climatic conditions the flora presents many features of interest. During the Permo-Carboniferous era the vegetation in Europe, parts of Asia, and the southern hemisphere was of a uniform type and included such genera as are familiar to students of the Coal-Measures flora of Britain. The comparatively small number of species obtained from the Permo-Carboniferous rocks in India, South Africa, South America, and Australia point to the existence of a flora characterised by the predominance of *Glossopteris* and *Gangamopteris* (usually spoken of as Ferns but probably Pteridosperms) with some other genera unrepresented in the northern flora and differing in the absence or rarity of many plants which form a characteristic feature in the Coal Measures of Europe and North America. The *Glossopteris* beds in India are spoken of by Geologists as Lower Gondwana, and Professor Suess instituted the name "Gondwana Land" for a former Southern Continent, now represented by S. Africa, S. America, Australia, and India, in which the *Glossopteris* flora flourished. The occurrence of ice-formed rocks in close association with the *Glossopteris* beds is frequently brought forward as evidence of different climatic conditions in the two Permo-Carboniferous botanical provinces and it is generally believed that the contrast between the floras is in large measure the expression of different climates. It is with questions relating to climate that M. Bertrand's paper is chiefly concerned.[1]

In his introduction to the account of the Falkland islands, Dr.

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[1] The distribution and the composition of the *Glossopteris* flora are fully dealt with by Mr. Arber in his valuable Monograph issued by the Trustees of the British Museum [Catalogue of the Fossil Plants of the *Glossopteris* Flora in the Department of Geology, British Museum (Natural History), 1905.] The subject was treated in less detail by the present reviewer in the Presidential Address to the botanical section of the British Association Meeting at Stockport in 1903. See also E. Koken, Indisches Perm und die permische Eiszeit. Neues Jahrb. für Mineralogie, Festband, 1906, p. 446.

Halle remarks that since Darwin's time, with the exception of some investigations made by members of the *Challenger* expedition in 1876, until the Swedish expedition visited the islands in 1901-1902, the geology of the islands has been almost entirely neglected. It was as a member of a smaller expedition undertaken by a few Swedish naturalists in 1907 that Dr. Halle made the discoveries with which this note is primarily concerned. Professor Andersson, the leader of the Swedish Polar Expedition (1901-1902), collected a few imperfectly preserved fossil plants, one of which is described by Professor Nathorst[1] as a species of *Phyllotheca*, an Equisetaceous genus characteristic of the *Glossopteris* flora of India and the Southern Hemisphere and recorded also from a few Palæozoic and Mesozoic strata in Europe. The occurrence of this genus suggested the forecast, justified by Halle's investigations, that other and more convincing evidence of the existence of the *Glassopteris* flora would probably be discovered in the Falkland islands.

A considerable portion of the islands is occupied by Devonian rocks from which a few fragmentary plants have been obtained. Some small pieces figured by Halle bear a fairly close resemblance to *Lepidodendron nothum* Ung. and *L. australe* McCoy, Lower Carboniferous and Devonian species. A point of general interest in regard to the occurrence of a marine Devonian fauna in the Falkland islands is that a similar fauna has been recorded from South Africa, Australia, and the Argentine Republic. It would appear, however, that the Falkland fauna is distinctly more closely allied to that of South Africa than to the fauna of the far nearer Devonian areas in South America. Dr. Halle discovered *Glossopteris* leaves and other genera characteristic of the *Glossopteris* flora at several localities in east Falkland and at the south point of Speedwell island. The presence of these plants points to correlation of the Falkland strata with the Lower Gondwana beds of India and other countries in which the *Glossopteris* flora existed.

Dr. Halle adopts the term Lafonian for the Falkland Gondwana series and from these beds he describes the following species :— *Phyllotheca australis* Brongn., represented by several imperfect pieces of stems and leaf-sheaths, in themselves hardly sufficient to establish the occurrence of the *Glossopteris* flora; another species of *Phyllotheca*, compared by Nathorst with the Siberian *P. deliquescens* Schmal.; *Glossopteris Browniana* Brongn. and *G. indica* Schimp. the commonest plants in the series; *Glossopteris angustifolia* Brongn. and *G. damudica* Feist.; *Gangamopteris cyclopteroides* Feist.; *Dadoxylon lafoniense* and some other less satisfactory forms too imperfect to be determined with certainty. As Halle points out, this flora is undoubtedly to be correlated with the Lower Gondwana flora of India, South Africa, Australia, and South America. It is customary in speaking of these southern plant-beds (in which the *Glossopteris* flora has been found) in terms of northern hemisphere stratigraphy to employ the comprehensive designation Permo-Carboniferous, as it is as a rule impossible to correlate them precisely with northern equivalents. The important point is that the rich flora from the Coal Measures of Europe and North America, which closely resembles that of the succeeding Permian period, is replaced in India and many regions south of the equator by one in which *Glossopteris* and *Ganagmopteris* are the most abundant genera, while most of the characteristic northern

[1] Nathorst, A. G., *Bull. Geol. Instit. Upsala*, Vol. VII, 1906.

types are unrepresented. It is noteworthy that *Lepidodendron* and *Sigillaria* occur in association with *Glossopteris* in South Africa and South America and the long strap-shaped leaves which are not uncommon in the *Glossopteris* beds and are usually assigned to *Neegerathiopsis* may be identical with the northern genus Cordaites. Making due allowance for the fact that authors are not infrequently led to give undue importance to wide geographical separation by the use of different names for very closely allied plants, and admitting that further research may connect more closely the Permo-Carboniferous floras on the two sides of the equator, the statement holds good that there is evidence of the existence of two more or less well-marked botanical provinces in the latter part of the Palæozoic era.

Dr. Halle gives an interesting account of the Lafonian glacial beds which occur immediately below the plant-bearing strata and shows clearly by his description of the rocks, some of which he speaks of as tillites (a term instituted by Professor Penck), and striated rock-floors that in the Falkland islands, as in other countries, where the *Glossopteris* flora occurs, sheets of ice were spread over the land surface of which the Falkland islands are a diminutive survival.

The question of the widespread ice-action in the southern hemisphere and in India in relation to the *Glossopteris* flora is dealt with by M. Paul Bertrand who gives a clear summary of the chief geological and botanical facts. After a brief reference to some of the hypotheses advanced by way of explanation of the glaciation during part of the Palæozoic period, he remarks that geologists have appealed for confirmation of their views to palæobotanists and to meterologists. Unfortunately, he adds, the study of Carboniferous and Permian floras instead of facilitating the solution of the problems raised by the association of the *Glossopteris* flora and ice-formed rocks, raises fresh difficulties. The fact that some of the northern genera such as *Lepidodendron* and *Sigillaria*, typical European Coal-Measure plants, grew in South Africa and South America in regions recently emerged from glacial conditions suggests the possibility that the vegetation of the Coal period north of the equator may have flourished in a temperate rather than in a tropical climate. He proceeds to quote certain conclusions regarded by some authors as favourable to this view, adding that if the northern flora grew in a temperate climate the lowering of temperature in the south, sufficient to bring about glacial conditions and to effect such a change in the vegetation as is revealed by a comparison of the two floras, need not be very great. There are, however, serious objections to the acceptance of the view that the nature of the Upper Carboniferous and Permian plants of Europe and North America is consistent with a temperate climate. M. Bertrand points out that it has been frequently asserted that *Lepidodendron* and other Carboniferous plants indicate by their anatomy adaptation to an environment physiologically dry ; but it is significant that the xylem elements in Lepidodendreæ are very much larger than those of recent conifers. The diameter of the tracheæ in the former varies from 100 to 125μ; in the latter from 20 to 25μ. In spite of the abundance of water which is suggested by the unusual size of the conducting channels, M. Bertrand adds, the Lepidodendreæ endeavoured to limit their transpiration. The stems possessed a thick covering of cork ; the leaves were reduced in breadth and

were protected against excessive loss of water by a hypodermal sheath of sclerenchyma and by a thick palisade tissue. The stomata were sunk in grooves. The opinion has been expressed that the xerophilous characters of the Coal-Measure plants may be the result of growth in salt water; but this would not account for all the facts. The occasional alternation of zones of crowded and more widely separated leaf-scars on Sigillarian stems may be the expression of variation in the rapidity of growth. The absence of regular rings of growth in the wood of *Lepidodendron* and other genera points to a uniformity of climate throughout the year. Dr. Gothan has recently written a short paper on the absence of annual rings in the stems of many Palæozoic plants and the bearing of this fact on questions of climate.[1] Without discussing his remarks on the main point, reference may be made to a criticism on the generally accepted view, adopted by Bertrand, namely that the occurrence of the *Glossopteris* flora in rocks closely associated with ice-formed material necessarily implies that the plants grew in a cold climate. He quotes the existence of a Mediterranean flora in the north of Italy on glacial moraines of the great ice age as an illustration of the falsity of the conclusions as to the *Glossopteris* flora. But it may be asked, is the conformable succession of Permo-Carboniferous glacial beds and the plant-bearing strata strictly comparable with the unconformable juxtaposition of the Mediterranean flora and the deposits of the ice age? The wide distribution of what has been called the boreal flora indicates an absence of climatic zones, and the temperature could hardly have been lower than that of our summer. The xerophytism of the Carboniferous plants, their rapid growth, and the large diameter of the tracheæ are regarded by Bertrand as evidence in favour of a tropical climate. On the other hand, in the southern hemisphere and in India there was extensive glaciation at a time when this presumably tropical flora flourished in the north.

The study of the structure of Palæozoic plants has made remarkable strides during the last few decades, but as yet little attention has been paid to anatomical data from a physiological or ecological standpoint. M. Bertrand's summary shows what contradictory results may be obtained from a cursory examination of anatomical evidence; it should also have the effect of stimulating palæobotanists to pursue a line of inquiry likely to yield interesting results and, incidentally, his paper emphasises the need for experimental work on recent plants. A good beginning has been made by Mr. Hamshaw Thomas in his investigation of the leaf-structure of *Calamites* which lead him to the conclusion that "the structure of the smaller leaves probably indicates that they grew in a moist situation, or where the atmosphere was humid. The larger leaves are more xeromorphic in character."[2]

In the concluding portion of his Presidential Address to the Botanical Section of the British Association Meeting at Portsmouth this year (1911) Professor Weiss gave an exceedingly interesting illustration of the application of data furnished by ecological investigations to the biology and ecology of the plants of the Coal period.   A.C.S.

[1] Die Jahresringlosikeit der palaozoischen Bäume und die Bedeutung dieser Erscheinung für die Beurteilung des Klimas dieser Perioden. *Naturwiss. Wochenschrift*, [N.F.], Bd. X., No. 28, 1911.

[2] On the leaves of *Calamites* (Calamocladus section). *Phil. Trans. R. Soc.*, Vol. 202, p. 51, 1911.

THE DISTRIBUTION OF THE FLORA IN THE

ALPINE ZONE.[1]

BY PAUL JACCARD,

Professor at the Federal Polytechnic, Zürich.

[WITH TWO TEXT-FIGS.]

THE botanising hitherto done in the Alps gives us but very imperfect information on the local distribution of the alpine flora. Attention has been specially directed to rare plants, whose least localities are recorded, while the common species are often neglected. But from the standpoint of the factors which regulate distribution the common species are the most important. The rare species of the alpine flora, those which appear only in a few isolated stations, sometimes only in a single one, are usually either species with a very sporadic general distribution, or they are endemic species, or finally they may be "glacial relicts." All these categories are of great interest from the standpoint of the history of floras ; their presence in the stations which they now occupy is explained not only by the ecological conditions they find in these stations, but also by historical causes, and especially by the conditions of post-glacial immigration.

Is the same true of the common species which form the basis of the vegetation of the Alps ?

In order to reply to this question I have considered, in an alpine district of fair size, various natural sub-divisions, presenting, besides numerous resemblances in their ecological conditions (*i.e.* conditions dependent on soil and climate), a few characteristic differences; and I have sought to determine, by comparison, the influence of these resemblances and differences on the composition of the flora.

I.

My researches have been chiefly carried out on three districts about fifty kilometres distant from one another.   These are :— (1) The upper basin of the Sallanche and of the Trient, (2) the *massif* of the Wildhorn, (3) the upper basin of the Dranses.

From the topographical point of view these three districts present great analogies: all three contain high summits covered with snow and ice : all three, except the northern slope of the Wildhorn, open to the valley of the Rhone: finally, owing to their proximity, the meteorological conditions appear very similar.

From the petrological standpoint, on the other hand, they are sharply dissimilar.   The *massif* of the Wildhorn is essentially calcareous ; the basin of the Trient includes both gneiss and limestone; while the basin of the Dranses presents the most various substrata, including the Casana schists, carboniferous schists, Antigorio gneiss, primitive rocks of the Mont Blanc series, calciferous triassic schists, etc.

Each of the three separate districts is sub-divided into parallel valleys, forming as many comparable sub-districts.

In making a complete list of all the species of plants met with in the alpine and niveal zones of each of these three districts, the following approximate numbers were obtained :—

1. Wildhorn (W)   -   350 species.
2. Trient (T)   -   470   „
3. Dranses (D)   -   600   „
4. The three together -   660   „

Of the 600 species of the basin of the Dranses, about 60 have not yet been met with in the other two districts : again of the 470 species of the Trient basin, about 60 are absent from D and W : finally about 30 species noted in W are absent from T and D.

In each case at least half the species noted in one of the

three districts, and absent from the two others, are common sub-alpine or woodland species, whose presence in one of the three districts to the exclusion of the two others is explained by the particular topographical configuration and by the greater or less continuity of the districts with the adjoining sub-alpine and lower zones.

About thirty are fairly common species in the Valaisian Alps, but are sometimes absent from considerable stretches of country, though it is impossible to explain such absence in one or another of the three districts by any special ecological conditions.

Finally, of the 660 species of the three districts, scarcely 40 are really *rare*, or are strictly localised either in the Alps composed of crystalline rocks (Pennine Alps and the *massif* of Mont Blanc), or in the calcareous Alps (western portion of the Bernese chain).

It seems then that the great majority of species (more than nine-tenths) might be met with in all three districts. But, as the annexed table shows, this is far from being the case.

Total numbers of species occurring in pairs of districts.

Trient and Dranses together	-	-	-	-	645
Wildhorn and Trient ,,	-	-	-	-	525
Wildhorn and Dranses ,,	-	-	-	-	647

Species common to two districts.		Percentage common to two districts.
Trient and Dranses - -	390	60
Wildhorn and Trient - -	295	56
Wildhorn and Dranses -	327	50

Each of the districts W, T and D thus possesses, besides the rare species mentioned above, a considerable number of species which are absent from *one* of the other two.

The ratio of the number of species common to two districts (T and D for example) to the total number of species collected in the two districts together (T + D), *i.e.*, their *coefficient of community*,[1] varies in the three cases given in the table between 50 and 60 per cent.

Thus in spite of their proximity and the similarity of their ecological conditions, the florulæ of our three districts possess very different compositions, and the comparative study of these

[1] $\dfrac{\text{Number of species common to the two districts}}{\text{Total number of species in the two districts}} \times 100$

Paul Jaccard.

florulæ shows that a great number of common species with a distribution through the entire chain of the Central Alps are actually absent over considerable stretches of country, while the conditions apparently capable of assuring their existence are everywhere realised.

We are thus led to ask whether the commonest species possess, like the rare species, a discontinuous distribution within the area of their occurrence.

In order to try and find a solution of this problem, a comparison was made, not of all the species of the districts W, T and D, but only of those constituting a single type of formation. For this purpose the alpine meadow above 1900 metres was chosen, and localities of equal area were selected, as closely similar as possible in respect of declivity, humidity and the general state of development of the flora.

The following is a list of these localities, with exposure, nature of substratum, and number of species collected in each case. The areas, averaging 3 to 4 hectares (say 7 to 10 acres each), the slope (20—30°) and altitude (between 1900 and 2400 metres), differ very slightly in the different cases.

	Locality.	Substratum.	Exposure.	Number of Species
1.	Plan la chaud, Val Ferret - -	Calciferous Triassic schists - -	West	101
2.	La Peulaz, Val Ferret - -	,, ,,	East	107
3.	South slope of Col Ferret - -	Lower Jurassic (with quartzites) - -	South-West	106
4.	Alpes des Tsesse-taz, Combe de La, Entremont - -	Dolomite - -	East	99
5.	Alpages des Vingt-Huit, Bagnes -	Calciferous Triassic schists and Casana schists - - -	West	140
6.	Barberine, Trient	Lower Jurassic lime-stone - -	South-West	114
7.	Luisin, Emaney -	Gneiss - - -	West	173
8.	Gagnerie, Salanfe	Upper Jurassic lime-stone - -	West	147
9.	Iffigen, Wildhorn	Cretaceous & num-mulitic limestone	South-East	147
10.	Küh-Dungel, Wild-horn - - -	,, ,,	North-East	150

From the standpoint of floristic richness these ten localities may be divided into two groups, five possessing about 100 to 114 species, the other five about 140 to 173.

But it is easy to satisfy oneself that the coefficients of community of different pairs do not depend on the number of species. The pairs of localities belonging to the first group (1—4, 6) possess in round numbers the following coefficients ;—

1 and 2	...	35%	2 and 3	...	36%	3 and 4	...	39%
1 and 3	...	40	2 and 4	...	26	3 and 6	...	27
1 and 4	...	40	2 and 6	...	30	4 and 6	...	27
1 and 6	...	21						

<div align="center">Average 32·1%</div>

The coefficients of the pairs of the second group are :—

5 and 7	...	30%	7 and 8	...	26%	8 and 9	...	31%
5 and 8	...	38	7 and 9	...	27	8 and 10	...	38
5 and 9	...	36	7 and 10	...	34	9 and 10	...	42
5 and 10	...	22						

<div align="center">Average 32·4%</div>

If the whole ten localities are taken in pairs the mean coefficient of the 45 pairs so obtained is also about 32% (actually 31·5%).

The lowest coefficient is 21% (between 1 with 101 species and 7 with 103) : the highest coefficients 39%, between 4 (99 species) and 9 (147 species): 40% between 1 (101 species) and 4 (99 species) ; and 42% between 9 (147 species) and 10 (150 species).

But if the values of the coefficients of community do not depend on the floristic richness of the localities compared, they must have a relation with ecological characters of localities, though it is often impossible to observe any strict proportion between the degree of ecological resemblance or dissimilarity and the value of the coefficients.

<div align="center">II.</div>

As a result of the comparison in pairs of our ten localities we have found that on the average a third of the species growing in two localities taken together are common to the two.

In face of the relative constancy of this coefficient of community we might suppose the existence of a group of ubiquitous species which are found in every locality and constitute a sort of permanent nucleus of community. *But this is not the case.* Of 370 species collected in our ten localities taken together, 108, or almost a third, have only been noted in a single locality, and 73, or about a fifth, in only two localities. There are only 10% of the

total number common to four localities, 3 to 4% common to six
localites, and 1 to 2% common to eight localities. Three species
only, *Gentiana excisa*, *Homogyne alpina* and *Nigritella angustifolia*,
or less than 1%, have been collected in each of the ten localities.
And meanwhile, what naturalist does not carry away from the
Alps the impression that the *majority* of the species of the alpine
meadows and swards are found everywhere ?   Close observation,
supplemented by careful statistical analysis, is necessary to con-
vince us of the infinitely various floristic composition of the alpine
meadow, and that different stations, in spite of physiognomic
uniformity, are in reality covered by very different plant associa-
tions. The fact is that besides the obvious ecological variations,
such as those of the degree of humidity, of slope, of exposure, and
of the chemical nature of the soil—variations which betray them-
selves in the plant covering by a comparatively small number of
formations (meadows, swards, rocks, screes, bogs, etc.)—there
exist many slighter variations of habitat, more difficult to appre-
ciate, which, in a station apparently uniform, create an infinite
diversity. The substratum especially, even the most homogenous
from the geological standpoint, may present in its chemical com-
position, in its structure, in its compactness, and in the thermal
and hygroscopic properties which depend upon these characters,
numerous differences which have their effect on floristic compo-
sition.

In this respect nothing is more instructive than the flora of
the summits of the southern Jura, of which the uppermost zone,
formed entirely of Kimmeridgian and Sequanian limestones, with
some outcrops of Argovian, possesses a remarkable petrographical
uniformity. All the summits are of about the same altitude,
between 1671 and 1723 metres : they are all situated on the
southern ridge of the Jura and present the greatest similarity in
regard to topographical conditions, especially in the direction,
force and frequency of the winds. Everywhere we have the same
turf-covered ridges, the same escarpments of white limetone, the
same dryness, accentuated by the same winds. And everywhere,
apart from some scattered Alpine and Mediterranean types, there
is a depressing floristic uniformity.

Yet in spite of this extraordinary apparent uniformity, any two
localities of approximately a hectare (say 2 acres), and each
separated by from two to ten kilometres, possess in common only
40 to 50% of the species collected on the two together.

The results obtained by comparing adjacent areas, each one square metre in extent, from one and the same meadow, are even more surprising. In a sub-alpine meadow at an altitude of 1,200 metres in the valley of the Ormonts (Alpes Vaudoises), where the species of 52 different square metres, each showing an average of 25 to 30 species, were enumerated, the proportion of species common to two adjacent square metres generally varied between 60 and 75%. Thus on two square metres, A and B, peopled by 38 species, only 25, or 66% were common to A and B.

The dominant conclusion which emerges from the facts given above, is *the infinite diversity of the alpine flora, and of the associations which constitute it*, a diversity so great that probably no two square metres of vegetation in the whole chain of the Alps, possess exactly the same floristic composition.

This diversity, which seems at first to escape all rule, really presents elements of regularity, which we have now to establish.

III.

Among the species which make up a plant covering, some are frequent, others less so, others again are very infrequent. These different degrees of frequency may be expressed by the four terms, *rare, somewhat rare, somewhat common* and *common*. These terms, as they are generally applied in the floras, are partly subjective, according to the degree to which the country to which they are applied has been explored, and to the judgment of the individual botanist who uses them.

It is however possible to give such terms a purely objective value. If an area be divided into four equal and comparable portions, those species found in only one may be called rare, those found in two, somewhat rare, those found in three, somewhat common, and those found in all four, common. Using this principle, all degrees of frequency that may be desired can be determined by increasing the number of divisions of the given area.

This method has been carried out for the 370 species collected on the 10 alpine meadows mentioned above, and for the 240 species noted on 12 localities of the pastures on the highest zone of the southern Jura.

For the former we obtain the following degrees of frequency expressed in percentages :—

Species noted in 1 locality	...	29%
,, ,, 2 ,,	...	20
,, ,, 3 ,,	...	12
,, ,, 4 ,,	...	9
,, ,, 5 ,,	...	8
,, ,, 6 .,	...	5
,, ,, 7 ,,	...	6
,, ,, 8 ,,	...	5
,, ,, 9 ,,	...	4·5
,, ,, 10 ,,	...	0·9

Fig. 1 shows the character of the curve corresponding to these figures (dotted line B). If the ten localities are grouped according to four degrees of frequency the following figures given below are obtained, and these give, in the graph, an almost straight line (B″) in which the irregularities of B disappear. The line B′ corresponds to five degrees of frequency.
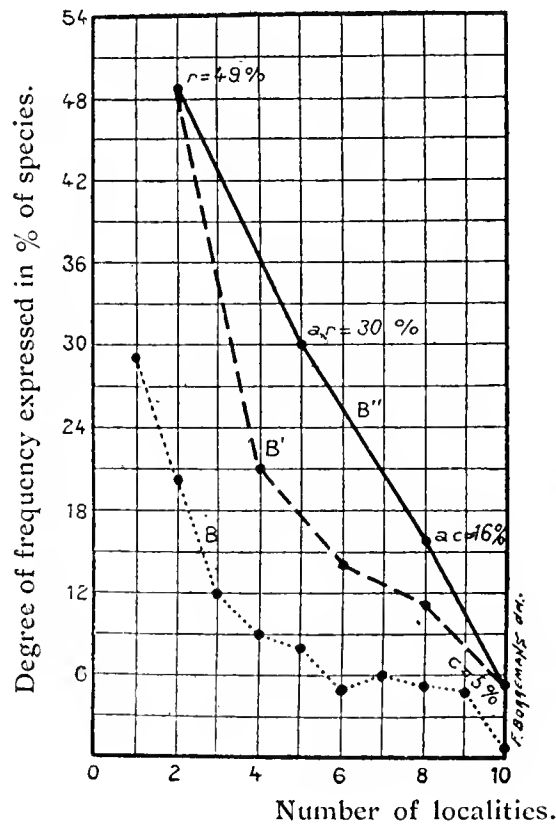
Fig. 1. Graph show- ing degree of frequency of 370 species of alpine meadow. B, B′ and B″ curves, corresponding with 10, 5 and 4 degrees of frequency.

Species noted in 1 and 2 localities (rare)	...	...	49%
,, ,, 3, 4 and 5 ,, (somewhat rare)			29
,, ., 6, 7 and 8 ,, (somewhat common)			16
,, ,, 9 and 10 ,, (common)	...		5·4

GATES—ŒNOTHERA.

Fig. 2 shows clearly that quite generally in the alpine zone the number of rare species is much the greatest and that of common species the least.
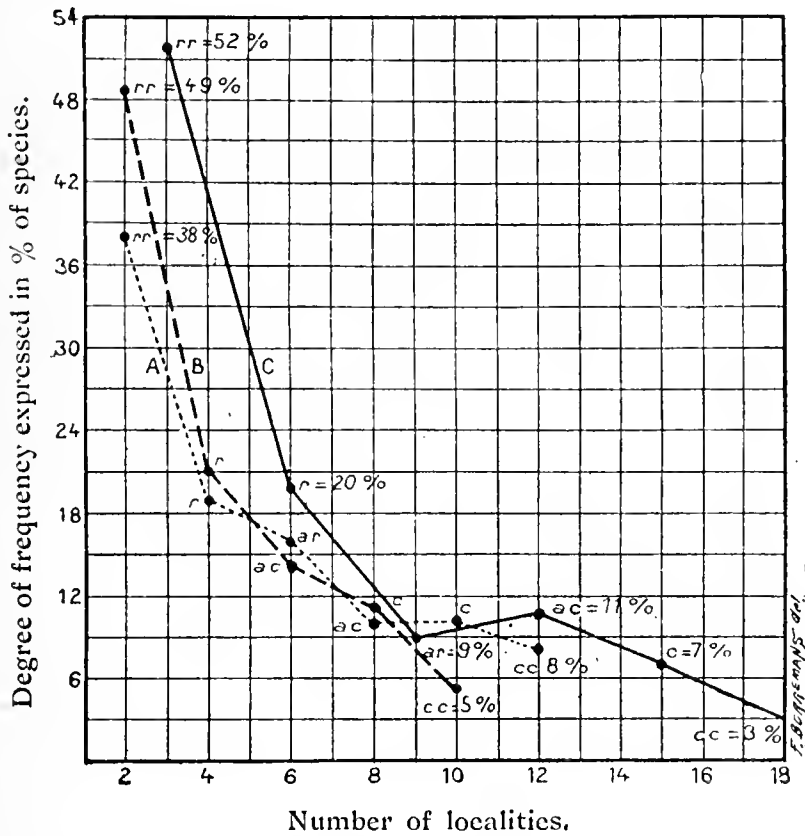
Fig, 2.   Graph showing relative proportion of species which are very rare (*rr*), rare (*r*), somewhat rare (*ar*), somewhat common (*ac*), common (*c*) and very common (*cc*).

A, in 240 species of the southern Jura.

B, in 370 species of the region W.T.D.

C, in 178 species of the Graian Alps (upper alpine zone).

It is impossible not to be struck by the resemblance between these graphs and the curves representing organic variation (Galtonian curves, binomial curves).   This resemblance would doubtless be still more marked if the number of species and localities considered were greater, and it may be supposed that in that case the curve expressing the different degrees of frequency of the associated species would correspond with a Galtonian "half-curve."   While awaiting its verification on a larger scale, the relation revealed derives special validity from the fact that it appears even in the distribution of a small number of species.

For the 92 species of the Ormonts meadow already mentioned the following figures are obtained : rare species, 60% : somewhat rare and somewhat common, 23% : common, 10%.

These figures confirm what has been said above, and enable us to conclude quite generally :—

(1). That in alpine grassland *rare species are the most numerous* (*numerous* not *frequent*) and common species the least numerous.

(2). That the *observed decrease in number in passing from the rare to the common species takes place according to a mathematical law of the same order as that which expresses the different degrees of frequency of organic variations.*

It is almost superfluous to remark that though the number of rare species exceeds that of the common ones, this is not true of the *individuals*, and that it is *the individuals belonging to the common species which are most numerous.*

The data necessary to determine the relative proportion of individuals according to the degree of frequency of the species to which they belong, in other words *individual frequency* in relation to *specific frequency*, are still lacking. But it can be seen that the curve of individual frequency will be contrary in direction to that of specific frequency.

To sum up, if we consider the commonest species of a given station as being the best adapted to the ecological conditions of that station, as being, so to say, the mean floristic expression, or that which realises the greatest number of individuals, we see that around this mean type of maximum individual frequency the others are distributed in decreasing numbers according to their decreasing degree of adaptation.

The local distribution of species on each limited portion of alpine grassland results then not only from the combination— essentially variable from point to point—of ecological factors capable of favouring or hindering the extension of competing species, but also from a factor of mathematical regularity, showing itself by the constant relation existing between the different degrees of frequency of species and of associated individuals. And, as we shall see, this factor of regularity is not the only one.

IV.

In determining for the districts of the Dranses, Wildhorn and Trient, or for wider or more restricted areas, the ratio of the number of genera to the number of species which enter into the composition of their flora, it may be shown that this ratio—which may be called the *generic coefficient*—varies within fairly wide limits. This is clear from the following table :—

	Number of Species.	Number of Genera.	Generic coefficient per cent.
Flora of Switzerland[1]	2453	659	27
„ Valais	1850	592	31
„ the region W.T.D.	661	221	33
„ upper basin of the Trient ...	470	211	45
„ 10 areas of alpine grassland ...	370	210	57
„ 12 areas of Jura grassland ...	240	141	60
„ 9 localities in Ormonts grassland	92	73	79
„ 1 area of Jura grassland ...	106	90	85

It has been demonstrated elsewhere[2] from a considerable number of examples that, generally, *the generic coefficient varies inversely with the variety of ecological conditions in the areas compared.* This is shown very clearly in the table given below, in which a a series is given in order of decreasing ecological diversity. The factors which have the most influence on the value of the generic coefficient are, as has been shown in one of the memoirs already mentioned, especially the extent, the topographical and petrographical complexity, the degree of isolation, and finally the latitude and altitude. In this place only the figures relating to altitude will be cited, since this factor is particularly seen in the composition of the alpine flora. The following figures, taken from data collected by Oswald Heer in his *Die nivale Flora der Schweiz*, are most convincing in this respect. They show that in the eight belts of 500' each established by Heer in the niveal zone of the Swiss Alps, above an altitude of 8000' (2600 metres),[3] the generic coefficient constantly increases as we pass to higher levels.

Belts (increasing altitude).		Number of Species.		Number of Genera.		Generic coefficient per 100 Species.
I.	...	338	...	139	...	41·4
II.	...	227	...	111	...	49
III.	...	153	...	78	...	51
IV.	...	122	...	68	...	55·7
V.	...	47	...	29	...	62
VI.	...	22	...	16	...	73
VII. VIII.	...	22	...	17	...	77·3

[1] The new Flora of Switzerland by Schinz and Keller indicates 2459 species and 660 genera: the generic coefficient is scarcely altered.

[2] Particularly in two of the memoirs whose titles are cited at the end of the article.

[3] 8530 English feet.

For the corresponding zones of the Graian Alps the generic coefficient is 53% between 2600 and 3200 metres, 69% between 3200 and 3500 metres.

We therefore conclude, generally, that *in the alpine zone the value of the generic coefficient increases with altitude*, or, in other words, that with increasing altitude the number of genera decreases less rapidly than the number of species.

This phenomenon, far from being the result of any specific influence of altitude, is in reality only a special case of the general law already stated relating the generic coefficient with the diversity of ecological conditions. It may in fact be established that in the degree that a station, such as alpine grassland for instance, becomes uniform, it becomes poor in species more rapidly than in genera. When the ecological uniformity is at its maximum the associated species almost all belong to different genera. But in the upper alpine zone, the increase of altitude, owing to its influence on the distribution of light, of heat, and of humidity, becomes a cause of ecological uniformity, and this is translated into terms of vegetation by the physiognomic uniformity of the vegetation of the heights. Only the species which have a close adaptation to such a habitat succeed in maintaining themselves. Among species of the same genus, only those persist which possess the most complete adaptation, to the exclusion of others, and so much so that most of the genera are represented only by a single species.

Thus we are led to conclude that the genus is not a more or less arbitrary taxonomic unit, but a biological entity whose value appears in the distribution of plant species in a state of intensive competition.

V.

This conclusion applies equally, though in a less absolute fashion, to the great sub-divisions, classes or orders of plants. It proves true in every case for the great sub-divisions Dialypetalæ and Gamopetalæ, whose generic coefficients show parallel variations, and are usually almost identical with the generic coefficient of the whole flora.

This appears in the following table :—

	The area W.T.D. 661 species.	Generic Coefficients of Jura meadow : 12 localities, 240 species.	Ormonts meadow : 9 localities, 92 species.
Dialypetalæ	33%	63%	76%
Gamopetalæ	33·6	63	74
Total Flora	33·4	61	79

In the first area containing 661 species, the agreement of the coefficients is surprising: in the second and third it is still very remarkable; and the fact that it manifests itself in such small numbers of species (240 and even 92) leads us to consider it as a fundamental law of distribution.

An examination of the floras of extensive areas (*e.g.*, Switzerland, France, Germany) shows that this agreement is quite general:—

	Germany 2500 sp.		Generic Coefficients of Switzerland 2450 sp.		France 4250 sp.
Dialypetalæ	...	28·3%	... 26·2%	...	19%
Gamopetalæ	...	28	... 26	...	19
Total Flora	...	28	... 26·4	...	19·7

The agreement which occurs, in areas whose extent and floristic richness are very different, between the generic coefficients of Dialypetalæ and Gamopetalæ and of the whole flora, seems to indicate that *the plants of these two classes have a sensibly equivalent power of adaptation, since in the competition which takes place among them for the conquest of ground, their different genera present a similar specific diversity.*

This being so, is it not legitimate to hold that in the struggle which takes place between them, individuals are not only the representatives of such and such a species more or less well adapted, but also the champions of higher biological groups, of genera, orders and classes, to which they secure a definite proportion in the entire distribution?

VI.

To sum up, analysis permits us to consider the distribution of plants in the alpine zone as a resultant of the combined action of three orders of factors: (1) *ecological factors* (nature of soil and climate); (2) *biological factors*, expressed by the degree of adaptation of species to their station, and better still by the *power of adaptation*, which is very unequal in different species; (3) *sociological factors* created by the competition which occurs between associated species.

The action of the first two factors has, as a consequence, in any station, the elimination of a certain number of species (eliminative selection). The third factor determines the local distribution of the species which are not eliminated (distributive selection).

This last kind of selection being at once numerical and taxonomic, we may distinguish: (1) A *numerical selection*, determining the *number* of individuals, and of associated species; (2) A *specific selection*, determining the nature of associated species, *i.e.* their

distribution among the genera, families, and classes to which they belong.

NOTE.—In order to avoid undue length a consideration of the other great sub-divisions of the plant kingdom is not entered upon here. Those readers who may be interested in such questions are referred to various memoirs in which they are discussed in detail ; among others :—

1. " Distribution florale dans une portion des Alpes et du Jura."
2. " Distribution de la flore alpine dans le bassin des Dranses, etc."
     Bulletin de la Soc. vaud. Sciences naturelles, Vol. XXXVI Lausanne, 1901.
3. " Lois de distribution florale dans la zone alpine." *Ibid,* Vol. XXXVII, 1902.
4. " Gesetze der Pflanzenverteilung." *Flora,* 1902.
5. " Nouvelles recherches sur la distribution florale." *Bull. Soc. vaud. sc. nat.,* 1908.
6. " Apropos du coefficient générique." *Ibid,* Procès-verbaux, Dec. 1908.

AN ONAGRACEOUS STEM WITHOUT INTERNODES.

By REGINALD R. GATES, M.A., PH.D.

[PLATES II AND III].

FOR several years I have been making analytical cultures of Œnotheras from the sandy coast of Lancashire. These North American forms are known to have been naturalized in this locality for at least a century,[1] where they have long been growing in large numbers. Bailey[2] and MacDougal[3] were the first to show that these forms contain what are now known as *O. Lamarckiana* Ser., together with certain forms corresponding to some of the mutants of De Vries' cultures, such as *O. lata* and *O. rubrinervis.* In subsequent cultures of a more detailed character I have found

[1] See Sowerby's English Botany, Vol. 22, pl. 1534, 1806.

[2] Bailey, Charles. " De Lamarck's Evening Primrose (*Œnothera Lamarckiana*) on the sandhills of St. Anne's-on-the-Sea, North Lancashire." Address to Manchester Field Club, January, 1907.

[3] MacDougal, Vail and Shull. "Mutations, variations and relationships of the Œnotheras." Carnegie Inst. Pub. No. 81, 1907.

that this colony of naturalized plants contains three general groups of forms : (1) *O. Lamarckiana*, which is almost if not quite indistinguishable from the race of De Vries' experiments and certain of De Vries' mutants, (2) a series of plants which are the same as *O. grandiflora* Ait. in cultures from one of its original localities, in Alabama, and (3) a considerable number of races having unexpected characters which are in many cases not inter-mediate between the *O. Lamarckiana* and *O. grandiflora* races. From a further analysis of this population of inter-breeding individuals, in comparison with other series of cultures of Œnothera races from various parts of the world, and by a comparison of their hereditary behaviour with that of related races whose origin is known, one may hope to learn something further regarding the manner of origin of these forms. And more particularly, it should be possible by such means to analyze the De Vriesian evolutionary factor of mutation, and discover in how far it is merely a process of hybrid splitting and in how far (as certain results show) it is a more deep-seated germinal disturbance, resulting in part from the effects of previous crossing, from the direct influence of changed environment, or from some internal and unknown cause.

Experiments dealing with these and related questions are still in progress, but the results are far too extensive to attempt to deal with in this communication, the purpose of which is merely to describe a peculiar development which occurred in one of my cultures of these Lancashire plants several years ago. A note on this subject was read at the Winnipeg meeting of the British Association[1] in 1909. The culture in question was grown entirely in the tropical greenhouse of the University of Chicago, the seeds being planted in July, 1907. Under these conditions of high temperature and high humidity, the plants belonging to the *O. grandiflora* series of forms remained rosettes until May, 1908, when they all formed shoots, and flowered during the following summer. But the 28 plants belonging to the *O. Lamarckiana* series of forms (which is more strongly biennial in habit than *O. grandiflora*) nearly all remained rosettes throughout the experiment, which lasted nearly two years, or until May, 1909. During this time, however, growth was continuous, new cycles of rosette leaves being continually added above while the older ones died away below. In this way a short stem was produced, without internodes and covered with leaf-bases in quincuncial arrangement. Plate II shows such

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[1] Rept. Brit. Ass., Winnipeg meeting, p. 677, London, 1910.

a case, in which the stem thus produced reached a height of six or eight inches, bearing a crown of rosette leaves at the top and giving a striking semblance to a cycad. The leaf-characters showed this plant (No. 6 of the culture) to be closely similar to, though not identical with, the mutant *O. lata.*

The plant (No. 25) figured in Plate III is probably of mixed ancestry, being partly from *O. Lamarckiana* and partly from *O·grandiflora* forms, if one can judge from its physiological behaviour, which was intermediate between that of these two species. That is, it remained a rosette for fifteen months, producing a considerable area of stem covered with leaf-bases, but finally, in October, 1908, formed a stalk with internodes and bore flowers. From pure seeds of this plant I have obtained a uniform race which breeds true in later generations. Its characters will be described in detail elsewhere. Its chief peculiarity is the very narrow leaves, while its bud characters are nearest *O. rubrinervis.*[1] This race maintains its intermediate behaviour between *O. Lamarckiana* and *O. grandiflora* as regards flowering and rosette formation under ordinary conditions of culture.

As is well known, the species of Œnothera which are ordinarily biennial can be grown as annuals by sowing the seeds in a greenhouse in winter and later transplanting out-of-doors. Under these conditions such species as *O. Lamarckiana,* *O. biennis* and their derivatives, produce a large rosette of many leaves before they finally send up a flowering shoot. When *O. grandiflora* is treated in this way, however, it frequently omits entirely the rosette stage, and produces a vertical shoot at once, or with only a few preliminary leaves corresponding to a rosette. The race (No. 25) referred to above possesses the same characteristic in a less marked degree, a certain number of the individuals omitting the rosette stage in each generation. The tendency to omit the rosette portion of the ontogeny under ordinary conditions of culture may thus be said to be partially inherited by this race.

A plant (No. 5) very similar to No. 6 in the tropical culture described above, produced finally a slender, fasciated and irregularly branched stem with flowers from which seeds were obtained. The resulting offspring, which were grown under ordinary cultural conditions, were a very heterogeneous lot, owing to the mixed ancestry of the parent plant, but none of them showed any inherited

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[1] See Gates. "Studies on the variability and heritability of pigmentation in Œnothera." Zeitschr. f. Abst.- u. Verer-bungslehre, Vol. 4, p. 350, 1911.

tendency to continue permanent rosettes and thus build up a "leaf-base area" as in Plate II.

Observations of this nature, dealing with characters which are most evident in their physiological manifestations, and showing the reactions of these characters under varying environmental conditions, emphasize the view that heredity and variation are but the two phases of a single process, namely, the interaction between the organism and its environment in every stage of its ontogeny. On the other hand, the cases now known from breeding experiments with plants and animals in which the same character may exhibit an inherited variation or mutation in certain cases and a similar non-inherited fluctuation in others, shows that there is a fundamental distinction between germinal and non-germinal variations.

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EXPLANATION OF PLATES II and III.

Illustrating Dr. R. R. Gates' Paper on "An Onagraceous Stem without Internodes."

Plate II. Lancashire Œnotheras. No. 6 of a culture kept growing for two years under tropical conditions. The rosette stage persists, thus producing a stem without internodes.

Plate III. Lancashire Œnotheras. No. 25 of tropical culture. After fifteen months' growth as a rosette it finally formed a shoot. See text.

THE INTERNATIONAL PHYTOGEOGRAPHICAL

EXCURSION IN THE BRITISH ISLES.

V.—The Killarney Woods

(Co. Kerry, Ireland).

It was a great delight to be invited to join the " I.P.E." through the British Isles and my high expectations were fully realised. I have to thank my British friends for this wonderful summer.

The present article is in reponse to a request from my friend Tansley to write a contribution for a souvenir-collection of impressions of the members of the party, and to choose any points which struck me most in the vegetation. Professor Cowles' general impressions (New Phyt., Jan., 1912, p. 25) are exactly mine, and the points Professor Massart has enumerated as those which struck him the most vividly, affected me in exactly the same way. I shall not repeat these impressions, but rather pick out from the numerous interesting things we saw the woods of Killarney, in Co. Kerry, Ireland, which strike me as distinctly subtropical in character, and compare them with similar woods I have visited.

We spent August 25th, 1911, a very enjoyable day, in the beautiful Oak-holly-woods near the Upper Lake of Killarney. The dominant tree is *Quercus sessiliflora* which reminds us that we are in north-western Europe. This is confirmed by a few of its associates such as *Betula pubescens*, *Salix cinerea*, *Prunus spinosa*, *Corylus*, etc. But these are quite accessory, the striking feature in this deciduous oak wood being the glittering, shining, effect produced by the reflection of light which takes place in the second layer of the wood. The smaller trees and the shrubs in fact have shiny leaves, and you fancy yourself in the southern country of evergreen *Laurel woods*. The holly, *Ilex Aquifolium*, is the general dominant, and specially contributes to this effect. Frequently interspersed and locally even dominant we find one of the most interesting woody plants of Ireland, the strawberry-tree, *Arbutus Unedo*, directing our thoughts to the West Mediterranean. This species embellishes the Killarney woods, not only as a shrub of 3-5 m. in height, as we are used to seeing it in Corsica, but as a tree of considerable height. The largest tree I saw, I judged to be 10 m. high, and this had a circumference of 180 cm. round the stem, taken 50 cm. above the ground, and 110 cm. taken at a height of 1 m. Another laurel-leaved plant, *Rhododendron ponticum*, catches your eye by its luxuriance. It is not native, but it spreads sub-spontaneously and evidently feels quite at home here. The many epiphytes give a nearly tropical aspect to the woods; the oaks bear epiphytically *Polypodium vulgare*, *Geranium Robertianum*, *Ilex Aquifolium* and *Saxifraga umbrosa*. Even *Rhododendron ponticum* ascends the lofty habitat of a branch of *Prunus spinosa*. Very striking also are the masses of the thin-leaved *Hymenophyllum tunbridgense* and *peltatum*; and in this fern-sward we find a plant of *Sedum album* !

When we look at the luxuriant heathy undergrowth, other

countries come to mind. *Calluna* bushes I measured had a height of about 2 m., the tallest I found was 220 cm. high, giving the illusion of a "Monte verde" of the Canaries, or of the mountain heaths of Corsica, where *Erica arborea* and other species cover great tracts of country.

How shall we account for all these phenomena? Let me give the plant-list I made in this wood and then try to find an explanation.

The Oak-holly-wood near the Upper Lake at Killarney had the following composition : (the underlying rock was Old Red Sandstone).

Quercus sessiliflora, d¹.
Ilex Aquifolium, sd.
Arbutus Unedo, f.
Rhododendron ponticum
   (subspontaneous), f.

Hedera Helix, a.
Viburnum Opulus, o.
Taxus baccata, o.

Hymenophyllum tunbridgense.

Betula pubescens.
Alnus rotundifolia.
Salix cinerea.

Hymenophyllum peltatum.

Prunus spinosa.
Corylus Avellana.
Sorbus aucuparia.

Calluna vulgaris, a.
Vaccinium Myrtillus, a.
Erica cinerea, o.

Pteridium aquilinum, a.
Ulex Gallii, o.

Luzula silvatica, sd.
Agrostis tennis, sd.
Sieglingia decumbens, ld.
Sphagnum acutifolium.
  „ *cymbifolium.*
Dryopteris Filix-mas.
  „ *æmula.*
  „ *spinulosa* sub-sp. *dilatata.*
Blechnum boreale.
Polypodium vulgare.
Osmunda regalis.
Anthoxanthum odoratum.
Brachypodium silvaticum.
Dactylis glomerata.
Molinia cœrulea.
Carex remota.
  „ *pallescens.*
Sedum album.
Saxifraga umbrosa, a.

Potentilla erecta.
Rubus spp.
Geranium Robertianum.
Oxalis Acetosella.
Euphorbia hiberna.
Viola silvestris v. *pseudomirabilis.*
  „ *palustris.*
Circæa lutetiana.
Sanicula europæa.
Teucrium Scorodonia.
Scutellaria minor.
Prunella vulgaris.
Veronica officinalis.
Melampyrum pratense v. *hians.*
Lonicera Periclymenum.
Succisa pratensis.
Knautia arvensis.
Solidago Virga-aurea.
Centaurea nigra.
Hypochoeris radicata.

Southwest Ireland has a *cool* and *very oceanic climate.* These two factors constitute a great difficulty in the study of the ecology of the vegetation, as this climate tends to " Cosmopolitanism," *i.e.* vegetation of very different range occurs together. Types of

¹d.=dominant; sd.=sub-dominant; a=abundant; f=frequent; o=occasional.

vegetation separated in a warm climate in several altitudinal belts converge and mix in cooler regions, because the basal vegetation extends northwards and at the same time the mountain vegetation descends more and more. In a continental climate the vegetation lines run far apart and each belt can easily be studied separately, while in the oceanic climate the lines merge ; for instance the alpine vegetation descends and mixes with montane or even with coastal plants.

To get the key for the cool oceanic Killarney woods we shall look for comparisons in a little warmer or a little less oceanic region.

Enjoying these beautiful Oak-holly-woods I was strongly reminded of similar communities I have studied in southern regions. What is united in Ireland is dispersed in the South in several belts. Let us compare the climate of Killarney with that of these regions I have in mind—the *Atlantic laurineous woods*, the " *Monte verde* " or *ericaecous scrub* of the *mountains of Teneriffe*, the *Beech-pine-holly-wood* and the *Arbutus scrub* of the *mountains of Corsica*.

Unfortunately meteorological data of all these regions are scarce, as Killarney has no old meteorological station and the stations of the southern regions compared are nearly all located in other than the desired mountain belts, but we can calculate the data approximately from those we have and from our own experience.

Killarney has a January isotherm[1] of about 7°C and a July isotherm of about 15·3°C, which gives an annual range of only 8½°C; frost is practically unknown : the rainfall is enormous, about 2000 mm. per annum, and the air nearly always moist. The climate of the laurel woods[2] and of the heaths of Teneriffe is very similar to that of Killarney, only a little warmer. Having no meteorological station in the woods we must start from the basal belt. Orotava at 100 m. has a mean temperature of 19·0°C, and a range of 8·7°C between the means of January and July (14·6°, 23·3°). The cloudy belt which bears the woods (between 500 and 1100 m.) and the heaths (between 500 and 1300 m.) may have means around 13°C, a little more than Killarney ; the extremes of monthly means about the same (8-9°C), perhaps a little less in the laurel wood, a little more in the heath, which is not quite so much centred in the cloud-belt. The relative humidity is very great, even the dry basal station of Orotava having a summer mean of 82%. The similarity is reflected in the vegetation. *Hymenophyllum tunbridgense*, *Polypodium vulgare*, *Pteridium aquilinum* are all present ; *Hedera Helix* creeps on the ground in masses. *Arbutus Unedo* is replaced by a near relative, *Arbutus canariensis* ; instead of *Ilex Aquifolium* we find the more southern species *Ilex canariensis* and *platyphyllos*, playing the same rôle. *Erica arborea* and other ericaceous shrubs take the place of the less heat-demanding *Calluna* and *Erica cinerea*. The relationship is clear : the similarity lies in the same oceanic climate, the difference in the temperature.

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[1] See map in R. Ll. Praeger : A tourist's flora of the west of Ireland, Dublin, 1909, p. 5.

[2] H. Schenck : Beiträge zur Kenntnis der Vegetation der Canarischen Inseln, 1907, and J. Hann : Handbuch der Klimalogie 1897,

To turn now to the Mediterranean. The pure Mediterranean climate is mild in winter but hot and dry in summer, especially on the coasts. Corsica is modified in the insular, *i.e.* oceanic, direction. For instance, the mean humidity of the year at Ajaccio is as high as 80%, dew is very frequent, the mean yearly temperature of 17·6°C varies from 10·2 to 25·6°C from January to July. Rainfall is small, about 630 mm. When we ascend the mountains the rainfall increases, the mean temperature diminishes and the extremes approach. The most luxuriant *Arbutus Unedo*-association we find from 200-700 m., where the insularity or oceanic character of the climate begins to be more pronounced. If we go higher up in the Corsican mountains we come to the Vizzavona Pass, with beautiful beech-holly-woods (900-1300 m.) which vividly remind us of Killarney. The winters are cooler than in Ireland, snow lies there for several months of the year. There is no *Arbutus*,[1] and of course no *Hymenophyllum*, but we still have the sub-dominant *Ilex Aquifolium*. Some plants of the undergrowth we meet again : *Pteridium, Sanicula europæa, Hedera, Polypodium, Teucrium Scorodonia*. The oak is replaced by the beech, the same phenomenon we see all over Europe, the oak as the tree of the pronounced oceanic climate ; the beech of medium moisture and moderate extremes of temperature, in other words the medium climate which we find in South-east England, in South Germany, the Swiss Plain and the Corsican mountains.

CONCLUSION.

The extreme oceanic character of the climate of Ireland, which brings the alpines down to the seashore, mixing them with southern plants, unites in the Killarney woods elements which in a warmer or less oceanic country form different formations in different altitudinal belts between 200 and 1400 m. The *Atlantic laurineous wood*, the *Canary heath*, the *insular Macchia* (this laurineous community contrasted with the continental *máquis* of sclerophyllous, hairy-leaved scrub), the *Corsican beech-holly-wood*, all show great affinities to the Irish *Quercetum sessilifloræ laurineum* or *Quercetum sessilifloræ aquifoliosum* as we might call it. This seems to me to be the key to the striking features of the Killarney woods which we enjoyed on our glorious trip through the British Isles on the International Phytogeographical Excursion of 1911.

ZÜRICH,   E. A. RÜBEL.

February, 1911.

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[1] M. Rikli (Botanische Reisestudien auf einer Frühlingsfahrt durch Korsika, 1907, p. 38) found the last *Arbutus* near Vizzavona at 850 m.

THE PAIRING OF THE CHROMOSOMES.

THE study of the method of pairing of the paternal and maternal chromosomes in meiosis has resolved itself of late years mainly into the elucidation of the question whether this union is brought about end to end or laterally,—in a telosynaptic or a parasynaptic manner. Theoretically it does not seem an affair of the first importance which of these processes takes place, nor need they be mutually exclusive; indeed it has been shown[1] that both may occur simultaneously in the same plant. The evidence, however, in favour of an end to end association for the most part suggests that this is achieved in the spore mother-cells, whereas many of those who have described lateral pairing hold that the approximation of homologous chromosomes takes place, not in the meiotic prophases but much earlier, so that a spireme, whose double character depends on the association of paternal and maternal threads, is present in the vegetative divisions.

A spireme of similar double appearance has been described by other observers[2] as due to the longitudinal fission of originally single structures, and there seems no doubt that this may be the case since a duplicate spireme has been reported in gametophytic nuclei where pairing of paternal and maternal elements is obviously impossible.

At the same time the account given of chromosomes which have become early associated in pairs is in certain cases exceedingly suggestive. Overton[3] for example has described twelve single chromosomes in the pollen nuclei of *Calycanthus floridus* in contrast to the twenty-four chromosomes arranged in twelve pairs which he finds in the sporophyte. He has observed a corresponding state of affairs in other Angiosperms also, and Harper[4] for *Phyllactinia* has described an association so intimate that the two chromosomes become an apparently single structure and the distinguishable number of chromosomes is unchanged by nuclear fusion.

[1] Digby, " The Somatic, Premeiotic and Meiotic Nuclear Divisions in *Galtonia candicans.*" Ann. Bot., 1910.

[2] Hof, " Histologische Studien an Vegetationspunkt." Bot. Centralbl., 1898. Digby, *loc. cit.* Fraser and Snell. " The Vegetative Divisions in *Vicia Faba.*" Ann. Bot., 1911.

[3] " On the Organisation of the Nuclei in the Pollen Mother-Cells of certain Plants with especial Reference to the Permanence of the Chromosomes." Ann. Bot., 1909.

[4] " Sexual Reproduction and the Organisation of the Nucleus in certain Mildews." Publ. Carnegie Inst., Washington, 1905.

From such evidence the possibility emerges that the homologous chromosomes may in some cases remain apart until meiosis has begun and may in others become associated in pairs at a very early stage of the life-history,—either at, or soon after fertilization. It is evidence in favour of the occurrence of an early association that certain examples have been lately reported of the arrangement of chromosomes in pairs during the prophase or on the spindle of the somatic divisions. This has been perhaps described most clearly by Müller[1] in the case of *Yucca*.

Indeed, though the presence of a double somatic spireme can by no means be taken as implying the approximation of paternal and maternal elements, it is not difficult to suppose that the stage of the life-history at which such association takes place may vary in different species.

We are aware of similar wide differences in the behaviour of the sexual nuclei. As a rule these fuse as soon as they come together, forming a single structure in which the two constituents cannot be discriminated ; in other cases, as in several of the Pinaceæ,[2] complete fusion is delayed until the first division of the oospore, or, as in certain animal embryos, till a considerably later stage ; or, finally, in the Uredineæ, the nuclei which become associated in the æcidium remain morphologically distinct throughout a long series of cell divisions and only unite at last on the eve of meiosis.

We are driven here to suppose that at some stage or other of the life-history an attraction arises between the gametic nuclei (or their equivalents) which is sufficiently powerful to bring them together within the same membrane. No doubt in primitive forms fusion of the nuclei immediately followed their association and was in its turn succeeded by reduction. The subsequent postponement of the reduction stage would leave a longer or shorter period during which each cell would contain the elements of two nuclei ; these would generally be united within one membrane, though throughout the sporophyte of the Uredineæ and in the early stages of some other forms they remain distinct.

With an increasing knowledge of the behaviour of the chromosomes it appears as though some gradations subsequent to fusion

[1] " Ueber Karyokinetische Bilder in den Wurzelspitzen von *Yucca*." Jahrb. wiss. Bot., 1909.

[2] V. H. Blackman, "On the Cytological Features of Fertilization and related Phenomena in *Pinus sylvestris*." Phil. Trans. Roy. Soc., 1898. Noren, " Ueber Befruchtung bei *Juniperus communis*." Arkiv. Bot. Svensk. Vetensk. Akad., 1904, etc.

might also be traced. Wherever gemini are formed we are bound to assume an attraction between homologous chromosomes sufficient to bring about the union of these in pairs. This attraction may supervene as soon as nuclear fusion has occurred (or at some stage shortly after) and may thus induce the formation of an apparently single structure as in *Phyllactinia* or of such a double spireme as Overton and others have described in the cells of the angiosperm sporophyte. The observations of Müller already referred to suggest that the members of each pair may remain in relation throughout the phases of vegetative mitosis.

In other cases it seems clear that the pairing of the chromosomes is postponed till the later prophases of the heterotype division; under these circumstances we shall not expect to find any evidence of chromosome association previous to the formation of the gemini.

The question must arise whether interaction or interchange between the paternal and maternal nuclear elements takes place more extensively when chromosome association occurs early than when it takes place only at the onset of meiosis. A study of the nuclear elements from this point of view would be of special interest in organisms where well-marked segregation of allelomorphic characters takes place. Indeed, it may be tentatively suggested that the clearest cases of Mendelian inheritance will perhaps be those correlated with a late association of the chromosomes in pairs.

H.C.I.F.

DEBARYA CRUCIATA : a Correction.

There are a few points in the description of *Debarya cruciata* sp. nov.[1] which require correction. I am indebted to Professor West for informing me of this. The material was mixed with a quantity of two species of *Mougeotia*, namely *M. gracillima* and a little *M. viridis*, and unfortunately the sterile cells of these were mistaken for those of the *Debarya*. The sterile cells of the latter were very scarce in the material, but revised measurements show that the filaments are thicker than those of *D. desmidioides* West. There are, moreover, always two pyrenoids in the chloroplast.

Although usually conjugation is between isolated cells of the filament, yet in a few cases zygospores are formed in contact.

A revised diagnosis is therefore appended:—
Debarya cruciata char. emend.

D. filamentis longis salpe dissociatis in cellulis singulis; cellulis vegetativis cylindricis, lateribus rectis, diametro 4-7-plo longioribus; chromatophoris cum pyrenoidibus 2.

[1] Price, S. R. New Phyt., Vol. X, p. 87.

Conjugatio vulgo inter cellulas singulas post dissociationem filamentarum, rarius inter cellulas duarum filamentarum sine dissociatione.

Zygosporis roturdo-quadratis, lateribus levissime retusis vel rarius rectis; angulis cornutis, cornubus cylindricis, solidis, apicibus ato-truncatis vel sub-truncatis.

Long cell veg.	...	38-50μ.	lat.	...	10-12μ.
„ zyg.	... ...	28-32μ.	„	...	20-24μ.
„ corn.	... ...	8-40μ.	„	...	10-12μ.

Hence Figs. 1 and 2, N.P., Vol. X, Pl. 2, are really figures of a *Mougeotia*, probably *M. gracillima*.

Professor West also informs me that the suggested comparison of the cruciate arrangement of the zygote with *Penium didymo-carpum* does not hold good.

Thus, as was stated before, the species is closely allied to *D. desmidioides*, West. The zygote characters are very similar, but the filaments are thicker and are not constricted as in that species.

The following reference with in penultimate para-graph, p. 89, was omitted :— West, W. " Monograph of British Desmids," 1904, Vol. I, p. 22.

S. R. PRICE.

NOTES ON RECENT LITERATURE.

PHYSIOLOGY.

THE METABOLISM OF TREES.

Ramann & Bauer. " Trockensubstanz, Stickstoff und Mineralstoffe von Baumarten während einer Vegetationsperiode." Jahrb. f. wiss. Bot., L, 1911, p. 67.

Bauer. Dissertation, München, 1910.

Ramann. "Mineralstoffgehalt von Baumblättern zur Tages- und zur Nachtzeit." Jahrb. f. wiss. Bot., 1911, p. 84.

RAMANN & BAUER have investigated, on a large scale, the variations of dry weight which occur in the one to four year old saplings of a number of trees during the year. They find that during the burst of activity following the spring awakening, while the leaves are expanding, a loss of 20—45% of the total dry weight occurs in the case of deciduous trees. This illustrates in a striking way the enormous expenditure of energy involved in

growth, a fact which is not always adequately realised. They found a smaller loss of substance, or even a small gain, for ever-greens such as the Conifers, which can begin earlier, by means of their old leaves, to make good the loss by respiration. In every case the stem, and still more the root, showed a loss due to translocation.

In commenting on the nature and conditions of the awakening of activity in spring, the authors suggest that the abundance of soil water and stored food lead to a sort of temporary over-feeding, with which the large-celled character of the spring wood is correlated, and think that the second burst of growth which often takes place later in the year (" Johannistriebe ") is often con-ditioned by an abundant water supply; in the latter case also a ring of " spring wood " is formed. They state, too, that in Scotch firs growing on rich lowland moors, where water and food-substances are abundant, the wood is almost all of the same character as the spring wood.

They have also investigated the variations in the amount of nitrogen and other mineral elements present in the saplings. With the single exception of the fir, they find that practically no nitrogen was absorbed during the spring while the leaves were expanding, and that the time of maximum absorption varied according to the species. In the alder, with its root-nodules, absorption of nitrogen continued steadily at a high rate from May to November. With respect to potassium, calcium, magnesium and phosphorus also they find that the time of maximum absorption varies for any given element from species to species ; while by the same species the various elements are absorbed at different times and at rates which vary independently. Thus the pine absorbs nitrogen most rapidly in June, calcium in August. Such results as these appear to demonsrate the extreme importance of the regulation of the mineral supply by selective absorption at the roots. They have, moreover, an important bearing on forestry, and may help ecologists to explain the common association of certain trees in the formation of woods.

Ramann, in a further paper, has dealt with the mineral content of leaves during day and night. With the exception of calcium, the various elements show merely fluctuating variations ; but calcium he found regularly more abundant during the night than during the day, whether calculated in terms of total dry weight or of the area of leaf-surface. His explanation of this is that translocation is more rapid during the day, and that calcium in some way or other participates in translocation. It must be pointed out that the former is purely an assumption, considering the present state of the evidence on the subject of translocation, and hence his inference with regard to the rôle of calcium is pre-mature and ill-founded. At present we do not even know with certainty that translocation occurs at all generally during the day ; and before any far-reaching conclusions are drawn as to the metabolic significance of any of the mineral elements, it is desirable that a closer investigation should be made into the changes in mineral content of the blade of the leaf, apart from the midrib and leaf-stalk, preferably by the half-leaf method.

HYDROGEN BACTERIA.

Lebedeff. " Über die Assimilation des Kohlenstoffes bei Wasserstoff-oxydierenden Bakterien." Ber. d. d. bot. Ges. XXVII, 1909, p. 598.

Niklewski. " Über die Wasserstoffoxydation durch Mikroorganismen." Jahrb. f. wiss. Bot., 1910, p. 113.

ANOTHER group of bacteria has lately been added to those capable of the chemosynthetic assimilation of CO_2. They appear to be of general occurrence in the soil and have the remarkable property of being able to oxidise free hydrogen in considerable quantity.

Lebedeff obtained what he considered pure cultures of such bacteria, and found that they could live either auto- or hetero-trophically. On inorganic media they obtained their carbon from CO_2, and the energy necessary for its assimilation by rapid oxidation of hydrogen, giving out at the same time some free nitrogen; when supplied with suitable organic substances less hydrogen was oxidised, and no nitrogen evolved. Lebedeff concludes that his results can be explained by supposing that the oxidation of hydrogen and assimilation of CO_2 are chemically independent, the latter having the same chemical basis as in photosynthesis. In old cultures the ratio of hydrogen to oxygen absorbed was just $2:1$ when allowance was made for the oxygen evolved in carbon-assimilation.

Niklewski was unable to obtain pure cultures of the bacteria on purely inorganic media, and among agar cultures found two distinct forms capable of oxidising hydrogen. He found Lebedeff's data insufficient for any comparison between his own and Lebedeff's bacteria or methods of culture. He found later that, separately, the two species develop fairly well on inorganic media in an atmosphere consisting chiefly of hydrogen, with a little air and CO_2. In the presence of more than 7—8% of oxygen neither developed alone, but if mixed together both flourished even in an explosive mixture of hydrogen and oxygen (33% O_2). Both appear to be obligate aërobes, although a trace of oxygen is sufficient for their existence on organic media.

In seeking for light on the mutual relations between these bacteria and their functions during symbiosis, Niklewski made cultures on various organic media in various atmospheres, with striking, but at present for the most part incomprehensible results. For instance he found that with one of the forms, *Hydrogenomonas vitrea* on glucose no hydrogen was oxidised, on mannite a considerable quantity was oxidised, on an acetate still more, *i.e.*, the better the food the less hydrogen was oxidised; but, in absence of CO_2, cultures grown on glucose oxidised hydrogen vigorously, while on the mannite and acetate there was no growth whatever. This may mean that CO_2 is necessary for the oxidation of hydrogen, enough being provided in the case of glucose by oxidation, but none from mannite or acetate. However this may be, Niklewski, in opposition to Lebedeff, regards the oxidation of hydrogen by these bacteria as an indirect process involving an

intermediate compound with CO_2, or with carbon reserves in the bacteria themselves. The evolution of free nitrogen, under certain conditions, is in his view an argument for the existence of complex relations.

As Niklewski's initial cultures showed, the presence of agar in the culture medium enabled either organism alone to develop in 30% oxygen; he also found that 0·1% of either potassium tartrate malate, or formate, after an initial delay in development, had a similar effect, either organism alone developing as well as under the best symbiotic conditions.

It is obvious that much remains to be done to solve the problems which Niklewski's work has opened up; to decide between his and Lebedeff's views on the physiology of these bacteria, and to explain the part they play in their natural habitat. It is not impossible that Lebedeff and Niklewski have obtained different bacteria, and that different relations hold for the different forms. D.T.

GENETICS.

INTER-RELATIONS OF GENETIC FACTORS.

Bateson & Punnett. "On the Inter-relations of Genetic Factors." Roy. Sce. Proe., B. Vol. 84, pp. 1—8, 1911.

Bateson & Punnett. "On Gametic Series involving Reduplication of eertain Terms." Journ. Geneties, Vol. 1, pp. 293—302, 1911.

RECENT investigations into the peculiar inter-relations which obtain between certain factors, when they are combined together in a hybrid, have given results of very great interest and significance, especially as regards their bearing on our conceptions of the nature of the phenomena which have hitherto been spoken of as " coupling " and " repulsion " of factors in the gametogenesis of hybrids.

The present position of our knowledge of these phenomena can be most easily explained if we follow Bateson and Punnett (see the first paper cited above) in tracing the steps by which it has been reached.

When a cross is made between parents differing in respect of two characters, A and B, the hybrid, which may be written AaBb, normally forms four kinds of gametes, namely AB, Ab, aB, ab.[1] In the simplest case these four kinds of gametes are produced in approximately equal numbers; but early in the investigation

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[1] A and B indieate the presenee ; and b the absence, of the factors which determine the eharacters.

of heredity in the Sweet Pea, it became clear that in certain cases there was a departure of a definite kind from this simple numerical relation. Eventually it became clear that this departure was such that the hybrid must be regarded as producing the four kinds of gametes in proportions represented by one or other of the series

$$3AB : 1Ab : 1aB : 3ab$$
$$7AB : 1Ab : 1aB : 7ab$$
$$15AB : 1Ab : 1aB : 15ab$$

or generally

$$(n-1) AB : 1Ab : (n-1) ab$$

where " n " is a power of 2.

Here, then, the gametes containing both factors are produced in greater numbers than those containing one or other but not both; this phenomenon was termed "partial gametic coupling" of the factors.

At the same time other cases were being discovered in which it appeared that the hybrid produced only two kinds of gametes, namely Ab and aB, each containing one, but not both, of the factors, which apparently never passed together into the same germ cell. This phenomenon was spoken of as "repulsion" or "spurious allelomorphism" between the factors. The offspring of a hybrid in which repulsion is taking place should be of three types, namely AaBb, AAbb and aaBB, which should occur in the ratio 2 : 1 : 1; since every gamete contains one or other factor, there should be no offspring of the type aabb. In several cases the results observed in large families conformed to these requirements; there were, however, one or two cases in which an isolated or occasional example of the double recessive, aabb, was encountered among the F_2-individuals. Speaking of certain of these cases, Bateson and Punnett[1] say " We incline to think . . . . that upon occasion the repulsion between factors may be imperfect, though whether this imperfection is sporadic, or whether it can be conceived as part of some scheme we do not yet know enough to say."

The next step was the discovery that the factors, A and B, which under certain circumstances are coupled, may under other circumstances be repelled in the gametogenesis of the hybrid; and it became clear that this difference in behaviour depends upon the distribution of the factors in the gametes to which the hybrid owes its origin. If the heterozygote, AaBb, is formed by the union of gametes, AB and ab, partial coupling occurs between A and B; if the heterozygote, AaBb, is formed by the union of gametes Ab and aB, repulsion takes place. For all cases of coupling, which it has been possible as yet to test, repulsion has been proved to occur when the cross is made in the appropriate form ; there still remain, however, several cases of repulsion which cannot yet be tested for coupling for lack of material, since the double recessive type, aabb, required for use as one of the parents, has not yet been encountered.

So far, although coupling had obviously shown itself to be partial, the results had suggested that repulsion, with a few sporadic exceptions, was complete. During last summer, however, a case

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[1] " The Inheritance of the Peculiar Pigmentation of the Silky Fowl." Journ. Genetics, I, p. 200, 1911.

was obtained in the Sweet Pea, in which it is quite clear that repulsion is partial also; that is to say, all four kinds of gametes are formed by the hybrid, but those bearing one or other factor alone are produced in greater numbers than those kinds containing respectively both factors or neither factor. The characters with which we are concerned in this case[1] are normal flowers (N) and fertile anthers (F), as contrasted with a peculiar malformation of the flower ("Cretin") (n) and sterile anthers (f). A Cretin fertile was crossed with various normal steriles. The F_2's from these crosses gave results which clearly show that the series of gametes produced by the heterozygote is 1NF : 3Nf : 3nF : 1nf. Such a series of ovules fertilized by a similar series of pollen grains would give 33 normal fertiles, 15 normal steriles, 15 cretin fertiles and 1 cretin sterile; the actual numbers obtained are 336 normal fertiles, 150 normal sterile, 143 cretin fertiles, 11 cretin steriles.

It will be noticed that when partial repulsion is of even such a low form as 1 : 3 : 3 : 1, only one double recessive, aabb, is to be expected in every 64 F_2-plants; as repulsion increases in intensity, zygotes of this form will become scarcer and scarcer, until under repulsion of the form corresponding to the highest form of coupling yet recognized, namely 1 : 127 : 127 : 1, only one such individual in every 65,536 F_2-individuals is to be expected; at the same time the zygotic types encountered in the F_2 approach more and more nearly to the ratio 2AB : 1Ab : 1aB, which would be given by complete repulsion. This being so, the principle of partial repulsion, discovered in the case just described, may almost certainly be extended to all cases of repulsion in plants and probably in animals also[2]; and at the same time the occasional occurrence of aabb-types in F_2's exhibiting repulsion, which was mentioned above, receives an explanation.

It therefore appears that the double heterozygote AaBb, may produce the four kinds of gametes in any one of the numerical ratios represented by the general expressions

$$
\begin{array}{cccc}
AB & Ab & aB & ab \\
(n{-}1) : & 1 : & 1 : & (n{-}1), \\
1 : & 1 : & 1 : & 1, \\
1 : & (n{-}1) : & (n{-}) : & 1.
\end{array}
$$

It is difficult to resist a speculation as to whether the ratios are always such that the smaller terms are to be represented by unity, or whether ratios may not occur of the form $(n{-}x) : x : x : (n{-}x)$ where x is *any* odd number less than n. As yet, however, no instances of ratios with $x > 1$ have been identified; in one or two cases, it is true, the constitution of the F_2's, as judged from the visible characters of the plants, is rather suggestive of a partial coupling or repulsion of a lower order than 3 : 1[3]; but, for

[1] See Bateson & Punnett. Journ. Genetics, I, p. 294, 1911.

[2] Bateson & Punnett do not commit themselves as regards the application to cases of repulsion in animals. see l.c. p. 301.

[3] See, for instance, Gregory, Journ. Genetics, I, pp. 125—129, 1911. The possibility there suggested, that the numbers observed in certain F_2's might be explained if partial coupling were found to take place in the gametes of one sex only, has been negatived by subsequent experiments, which have shewn that both ovules and pollen grains form coupled series (see Roy. Soc. Proc. B, 84, p. 14, Table II).

various reasons, the evidence to be gained from these cases is by no means conclusive, and the question must be left for further experiment to decide.

The results outlined above open up several interesting problems, for a discussion of which the reader must be referred to Bateson and Punnett's paper cited at the head of this article. It is only possible here to mention one or two more important points. In the first place comes the question as to how these gametic systems are formed. No simple system of dichotomies could provide the observed ratios, and it is scarcely possible to imagine how a series involving 256 terms could be provided for in the maturation divisions of the ovary of such a plant as the Sweet Pea. There is, moreover, evidence from other sources which indicates that segregation may occur at an earlier stage than the actual divisions of sporogenesis or gametogenesis.[1]

Further, the fact that the heterozygote AB.ab shows coupling, while the heterozygote Ab.aB shows repulsion, suggests that the difference in behaviour may be a consequence of the difference in the geometrical positions of the factors relative to the planes of some critical division or divisions. If the original cell, in the divisions of which segregation takes place, be imagined to give rise to four quadrants, representing the four kinds of gametes, the increase in number of two of the types may be imagined as due to the proliferation of an opposite pair of quadrants, by a series of periclinal and anticlinal divisions such as would readily give the numbers characteristic of coupled systems.[2] If the numerical preponderance of two kinds of gametes be due to processes of this kind, it is clear that factors which are distributed according to one of these systems cannot be segregated simultaneously with other factors which are distributed on the normal Mendelian system.

From what has been said above it is evident that the terms " coupling " and " repulsion " imply a conception which is no longer justified. " Coupling " was introduced to denote association, " repulsion " the disassociation of special factors. The phenomena are, however, now seen to be due to the production of an excess of certain kinds of cells, and Bateson and Punnett suggest that such cases may be conveniently referred to as the " reduplication " of certain terms in a series of gametes.

In conclusion, reference must be made to the existence of systems of *three* factors. Cases are known in which two factors may be severally coupled with a third factor, and results of great interest may be looked for from investigations into the genetic properties of plants heterozygous for all three factors.

R.P.G.

[1] E. R. Saunders. Rep. Evol. Com., Roy. Soc. IV, pp. 36—40, 1908; Journ. Genetics, I, pp. 60—64 and p. 304, ff. 1911. de Vries. Biol. Centralbl., XXXI, p. 97, 1911.

[2] For a further explanation of this conception the reader is referred to Bateson and Punnett's article in the Journ. Genetics, Vol. I, pp. 299 ff.

Four Books on Heredity.

Baür, E. " Einführung in die experimentelle Vererbungslehre," pp. iv + 293, with 80 Text-figures and 9 coloured Plates.   Berlin, Borntraeger, 1911, Paper, 8m, 50pf., Linen, 10 marks.

Haecker, Valentin. "Allgemeine Vererbungslehre," pp. x + 392, with 135 Text-figures and 4 coloured Plates.   Braunschweig, F. Vieweg, 1911. Linen, 15 marks.

Goldschmidt, R. "Einführung in die Vererbungswissenschaft," pp. ix + 502, with 161 figures.   Leipzig, W. Englemann, 1911.   Lincn, 12m. 50pf.

Darbishire, A. D. " Breeding and the Mendelian Discovery," pp. xii + 282, with illustrations in colour and black and white.   London, Cassell, 1911. Linen, 7s. 6d.

As the title indicates, and as those who know his work would expect, Baür deals with the experimental side of the study of Heredity, and is content to indicate in a few pages the trend of the ideas which have been developed by cytologists in their endeavours to relate the phenomena of genetics to observations on the structure of the cell.   It is scarcely necessary to say that Baür covers the ground he has marked out in a thorough and comprehensive manner ; perhaps the chapters on Variegation and on Graft-hybrids, in the elucidation of which Baür has himself played so large a part, may be singled out for special mention.   For illustrating many of the phenomena which he describes, he relies largely on examples drawn from his own work on *Antirrhinum*, which are illustrated by several good coloured plates.   Professor Baür is to be very heartily congratulated on his delightfully clear and lucid exposition of his subject.   The book is called an " Intro- duction " and amply fulfils all that is required of it under that head ; but it is more than that, and it will be welcomed by everyone who is interested in the study of Genetics, partly because it contains some new results not published elsewhere, but partly, and perhaps chiefly, because it has a certain charm of personality, which is best explained by the motto which Baür has adopted from Sachs, " Wer aber Vorlesungen hält, hat nicht nur das Recht, sondern auch die Pflicht, seine eigenste Auffassung des Gegenstandes in den Vordergrund zu stellen. ..."

The standpoint of Haecker, a cytologist and zoologist, is reflected in the treatment of the various subjects included in his "Allgemeine Vererbungslehre."   Here cytological observations are dealt with fully, and, compared with Baür's work, the treatment of the experimental side is less detailed and is illustrated largely by reference to animals.   The two books are, therefore, to some extent complementary to one another.   Haecker adopts the historical method of dealing with his subject; this method has advantages, but it entails a certain interruption of sequence in passing from cytology to experimental work and back again, Whatever defect may result therefrom is, however, greatly minimised by the division of the book into Parts, corresponding with the principal divisions of the subject,

Haecker's book vies with Baür's in clearness and lucidity.   The

author contrives to give a clear and connected account of the more intricate parts of his subject by means of a judicious selection of illustrative examples and the use of copious footnotes and references to facts and observations, deserving of notice, but subsidiary to the main line of argument.

Goldschmidt claims for his "Einführung in die Vererbungs-wissenschaft" no more than that it should present such a selection of material as will serve to illustrate all essential facts by at least one example. In spite of the modesty of this claim, the book contains a mass of information, certain aspects of the subject being treated more fully than by either Baür or Haecker. At first sight the book has rather a formidable appearance with its long unbroken paragraphs, and the effect is heightened by the absence of headlines to the pages (for one who confesses to a constitutional dislike to using the index this is a serious matter). The impression so produced soon disappears as one reads; Goldschmidt puts his case clearly and carefully, but a more rigorous selection of material might, perhaps, have been advantageous in a book which is intended to be read straight through, while the method of citing authorities is not sufficiently precise for a book of reference. Thus, if one is anxious to consult a paper cited by Goldschmidt, one turns up the author's name in the list of literature (a very copious one) with the risk of finding that the titles of the several papers cited do not give a sufficient guide to enable one to distinguish the article which is being sought.

Mr. Darbishire's book is of a different kind altogether from those noticed above. It provides an introduction to the facts discovered by Mendel, and their bearing upon the science of heredity, by opening the door "to an intimate familiarity with a few instances of the Mendelian phenomenon, and especially with those studied by Mendel himself. To this end I have given a fuller account of the phenomena discovered by Mendel than has yet appeared in popular form: the seven pairs of characters studied by him are all figured for the first time . . . ."

Mr. Darbishire writes fluently but the book is not conspicuous for its simplicity or clearness. For ourselves, we have not found the author's treatment of the problems which he discusses to be very illuminating, and we fear that the reader who makes his first acquaintance with Mendelism through Mr. Darbishire's book may find some of his impressions a little vague. The illustrations are good and are fully adequate to the matter provided in the text, which receives a generous allowance of space in its 274 pages.

R.P.G.

THE SCOTTISH BOTANICAL REVIEW.

THE first number of this new quarterly periodical (with which are incorporated the Transactions of the Botanical Society of Edinburgh) has recently appeared. It is edited by Mr. Mᶜ Taggart Cowan, Jr., with the assistance of some well-known authorities in floristic and ecological botany: Messrs. William Barclay, Arthur Bennett, A. W. Borthwick, R. H. Meldrum, W. G. Smith and James Stirton. It contains original memoirs, general articles, reviews and notes extending to 56 pages in all. The Review is priced at 2/6 (annual subscription 7/6), and is published by Neill & Co., Bellevue, Edinburgh. The typography is excellent.

The new Review makes a capital start, and if it maintains its standard will prove an exceptionally interesting addition to the periodical literature devoted to "outdoor" botany.

The first item is the first instalment of a memoir by Mr. C. B. Crampton, of the Geological Survey, on "The Geological Relations of Stable and Migratory Plant Formations." When complete we hope to notice this paper again. It contains some valuable criticisms of current conceptions of plant formations and some interesting suggestions with regard to their classification.

Mr. Arthur Bennett writes on "Aquatic Forms and Aquatic Species of the British Flora," stimulated thereto by the recent visits to this country of Dr. Glück of Heidelberg and Professor Rothert of Cracow and by Mr. G. West's recent work on the Flora of Scottish Lochs.

Dr. Borthwick contributes a very interesting article on "Some Modern Aspects of Applied Botany," in which he directs attention to those aspects of modern scientific botany which have a clear practical application, specially instancing ecology, physiology, and pathology. He gives numerous instances of the enormous monetary losses caused by plant-diseases and the successful efforts which have recently been made to combat them. One very remarkable instance is that of the disease of the Weymouth Pine (*P. strobus*), which was introduced into the States with *European* seedlings of the Weymouth or "White" Pine, which is an abundant American native tree! But the Americans are fully alive to the importance of organised scientific research on plant-diseases, and of the organisation also of *immediate* application of preventive measures, when these are possible; and they will probably stamp out this particular disease. In the case of the chestnut bark disease they have not been so fortunate, and this fungus is said to be threatening to destroy chestnut cultivation in the States. Our own Government has recently taken important steps in the right direction through the funds made available by the Development Act of 1909, and we may now expect rapid development of the study and prevention of plant-disease in this country.

As regards the practical application of ecology, even in the present rudimentary condition of the subject much might be done by insisting on the planting of the appropriate species or variety of forest tree in place of those which can never succeed under the conditions they are called on to support. Dr. Borthwick mentions the case of the Scots Pine, which is said to show several well-marked

constant varieties adapted to different habitats ; and the case of the two British oaks is another which might be mentioned.

A useful little paper by Mr. Miller Johnson on " Ecological Terminology as applied to Marine Algæ," deals with a department of synecological research which has as yet been very little developed in this country, though several beginnings have been made.

The rest of the Review is occupied by floristic notes, notices of books and papers, etc. Among the reviews is an appreciative notice of "Types of British Vegetation," containing some intelligent criticism. We may point out that the work is cited as " *The* Types of British Vegetation," whereas the first word is lacking in the proper title. This may seem a very small point, but the definite article was advisedly omitted in naming the book, in order to avoid any suggestion that the work included *all* existing types, a suggestion which would have been misleading.

A.G.T.

LABORATORY NOTES.

A Method of Staining Microtomed Sections in the Ribbon.

In these days of the microtome it is often desirable to ascertain the condition of the tissues and generally to view the structure of the member embedded in the paraffin before proceeding entirely to cut up the block. The method commonly employed is the usual one of floating out a piece of the ribbon, drying, dissolving the paraffin in xylol, and so on. And this, no doubt, is a very good way but it has the disadvantage of taking up much time.

The following method, which does not appear to be generally known, answers admirably; it was shown me many years ago by Martin Woodward, a past master of technique, and we were employed in perfecting and extending it to double-staining when his untimely death put an end to the investigation.

The ribbon is floated out on the prepared slip, not with water, but with an aqueous solution of safranin, gentian violet, or with many other aniline dyes. When quite flat, the superfluous stain is drained off and the slide is allowed to dry; on dissolving off the wax with xylol, the sections are found to be stained and it is only necessary to mount in canada balsam. The depth to which the section is stained depends on the strength of the solution used and the time of exposure to its action. If it be found that the preparations are overstained the slide may be rinsed, after the removal of the wax, for a few seconds in a mixture of equal parts of absolute alcohol and xylol, then cleared in xylol and mounted in balsam. No general rules regarding the strength of the stain and the time of exposure can be laid down; so much depends on the tissues used, but a little practice soon enables one to stain so nicely that no washing out or restaining is required.

The whole process hardly takes a minute to perform and herein lies its great value. The aniline dyes are the most satisfactory; hæmatoxylin, as far as has been seen, gives very poor results. If

convenient, stains dissolved in alcohol may be used; but greater care is necessary, for the alcohol may catch alight, and also the sections shew a tendency to wash off the slide.

The method opens up many questions regarding the physical chemistry of staining; for instance, why should sections embedded in paraffin stain so much more quickly than when the wax is removed. Of course, a hot dye will stain more quickly than when cold, but the increase in temperature does not by any means entirely account for the phenomenon in the above method. It is possible that the mode of presentation of the dye is important: the solid paraffin consists of innumerable crystals separated one from the other by very minute capillary spaces, so that when the microtomed ribbon is floated on the solution of the stain, the pigment is presumably presented to the tissues in innumerable capillary columns. Has this, if true, anything to do with the phenomenon?

It may also be noted that many dyes, safranin for example, stain the tissues generally, not merely the lignified and cuticularized walls only.   T. G. HILL.

Scharlack R: A Microchemical Test for Oils.

The usual microchemical reagents for oils are osmic acid and tincture of alkannin: both are unsatisfactory, the former is expensive, does not keep any length of time and stains other reserve food-materials in addition to the oils; the latter to give entirely satisfactory results should be freshly prepared from the root of *Alkanna tinctoria*, which is inconvenient.

While working at St. Thomas's Hospital it was noticed that sections of certain pathological tissues, (amylosis of the liver?) were stained with Scharlack R. to contrast the particular feature. On trying this reagent with many oil-containing seeds, *e.g.*, sunflower, hemp, castor oil, etc., it was found that the oil globules speedily absorbed the dye and were stained a bright pink; in fact, it appears an excellent reagent, has been used in my practical classes for several years, and has never failed. So far as has been seen it does not deteriorate with age; further, it is easy to make up and its reaction is characteristic. To prepare it, make a saturated solution of the solid stain (Grübler's) in a mixture of 70 parts of absolute alcohol and 30 parts of water by volume. When the solvent will take up no more stain, filter and keep in a glass stoppered bottle. For use, mount the section, or the scraping of the seed, in a drop or two of the Scharlack R. In a very short time the stain will all be absorbed by the oils which will be coloured a bright pink: Protein bodies and starch grains are unaffected, and, with regard to membranes, cellulose and lignified walls remain unstained whilst cuticle stains a bright pink.

Sudan III similarly prepared and used will give like results.

T. G. HILL.

THE SHINGLE BEACH AS A PLANT HABITAT,

BY F. W. OLIVER.

[PLATE IV AND EIGHT FIGURES IN THE TEXT].

IN approaching the subject of Maritime Shingle as a Plant Habitat, a preliminary and general exploration of the field may perhaps be permissible. For, unlike the analogous habitat of the sand dune in its relation to vegetation, the shingle beach has largely escaped the attention of botanists. On the northern and western shores of Continental Europe the wandering dune long ago asserted itself as an economic problem of the first magnitude, the solution of which was to be reached only by systematic and continuous study directed by appropriate state-organised departments. Shingle, however, has enjoyed no such treatment—probably because its occurrence is a minor episode in the coastal phenomena of the countries in question.

On the British coasts shingle forms a not inconsiderable part of the drift which circulates on our shores[1] and the problems which arise in connection with it—geological, physical and botanical—are no less worthy of study for their own sake than those of the dune; whilst the high importance of coastal drift as a defence against the wasting of the shore line has been sufficiently emphasized by the recent " Report of the Royal Commission on Coast Erosion."[2]

The intention of the present article is not, however, to deal with the economic problems involved, but rather to outline the general topographical and physical characteristics of shingle beaches as an introduction to a more purely botanical treatment of the subject.

[1] Not far short of 300 miles of the coast-line of England and Wales is lined by shingle.

[2] London, 1907.

Though the illustrations given here are mainly drawn from the more accessible aggregations of shingle occurring on the east and south coasts of England, it is not anticipated that these will be found other than representative of this type of formation generally.

The Main Types of Shingle Beach.

Shingle banks arise on our coasts when suitable materials from the waste of the shore, such as flints, find their way into the zone of the littoral currents. In these shallow waters they are kept continually on the move by the waves, whilst in obedience to the more or less constant currents they are drifted in certain definite directions. The raising of these materials to form banks or beaches above high-water mark is the work of the waves and is promoted especially by heavy on-shore gales.

The form assumed by these banks shows considerable diversity, and it will be convenient first to discriminate between what may be termed the principal morphological types of shingle banks.

1. *The Fringing type.* This is the simplest case, the shingle being directed by the shore current and forming a strip in contact with the land along the top of the beach. This type is well illustrated at many points on the south coast of England, notably on the coast of Sussex, and on the opposite shore of the Channel, *e.g.*, S.W. of Dieppe.

When the current leaves the shore other types are produced.

2. *The Shingle Spit.* This is produced when a coast-line suddenly changes its direction, turning landward, whilst the current pursues its original course, so that it separates from the shore. The drifted shingle accumulates along the line of the current to form a bank or causeway often reaching a length of several miles. This type is attached to the shore at the point where the current leaves it and then runs straight or with a gentle curvature to its distal, growing extremity. The apex of this type is particularly liable to deflection as a landward hook (Text-figs. 3 and 4).

Examples: Hurst Castle Bank; Blakeney Bank.

3. When a shingle spit once more reaches the land it is distinguished as a *bar*. The Chesil Bank, Dorset, would appear at first sight to belong to this category, but as the sequel will show, the exact status of this bank is still a matter of discussion by geologists (Text-fig. 5).

4. *The Apposition type.* Sometimes the current becoming modified proves inadequate to transport the drift to the end of a bank or beach, or the apex has become deflected in the landward direction so that the littoral current cannot reach it. From these, or analogous causes, the material will be deposited on the flank, where it will accumulate till lifted outside tidal limits as the result of an exceptionally high tide caused by a gale. In this way a succession of closely approximated, more or less, parallel banks may be thrown up, one behind another, with the result that very extensive areas of shingle are produced (Text-fig. 1).
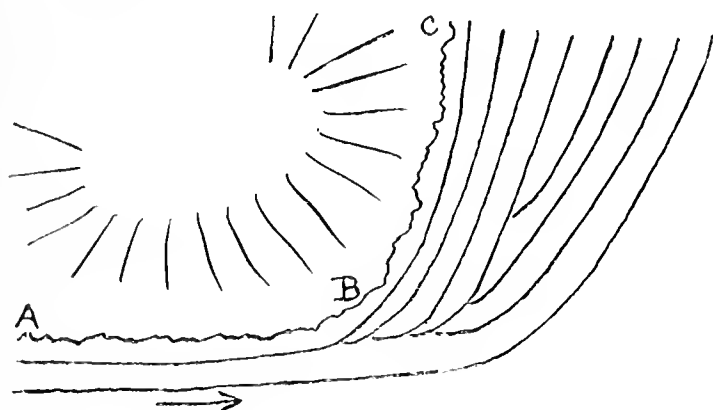
Fig. 1. Apposition type of shingle bank. A, B, C, is a point of land; the arrow marks the direction of coastal drift ; the successive shingle banks lie to the right of the figure : modified from F. Drew.

The outstanding example of this type is Dungeness, but a localised growth by apposition is by no means uncommon on the banks of the spit type, as is well illustrated at Blakeney.

Several types additional to the above have been distinguished by American geologists who have made a detailed study of the shores of their pleistocene lakes, but it is not necessary for the present purpose further to elaborate the types.

In the present paper we shall deal more particularly with the *shingle spit* and its modifications. This and the fringing type are of most frequent occurrence in England, and a sketch of the salient features of the spit will serve as a convenient introduction to the ecology of shingle.

General Features of the Shingle Spit.

In this type the point on the mainland at which the spit leaves the shore is a salient angle—a point at which the coast-line trends landwards owing to the presence of an estuary or other analogous feature. The axis of the bank continues the direction of that portion of the shore-line along which the supplies of shingle drift.

The bank may run straight, but more usually it is gently curved—the convex face being presented to the sea.

As a rule this type runs at some distance from the shore-line, the protected area between bank and shore being occupied by salt marshes subject to the tides.

In effect these salt-marshes form a littoral shelf, of varying-width, along the outer edge of which the shingle rests (Text-fig. 2).
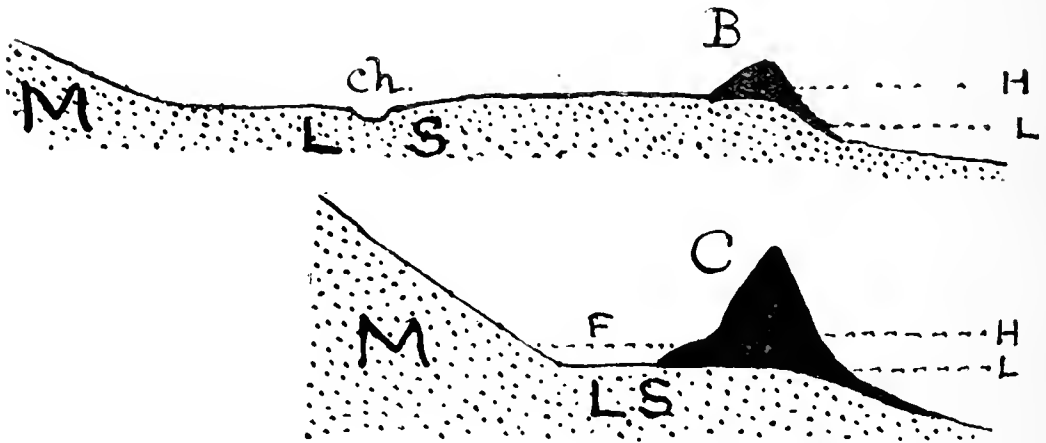
Fig. 2.   Diagrammatic sections of Blakeney Bank (B) and Chesil Bank (C) to show the relation of the shingle to the littoral shelf (L.S.) and mainland (M)   Ch, channel ; F, water level of Fleet ; H and L, high and low tide-marks.   The shingle is drawn black.   The vertical scale is much exaggerated.

As a consequence of their sheltered position such marshes offer facilities for reclamation by the construction of earthen mounds or banks at right angles to the shore, and high enough to exclude the tides. In cases in which advantage has been taken of these facilities the shingle spit acquires some economic importance, for much depends upon its stability as the bulwark of the reclaimed area.

Hook-Formation.

The majority of shingle spits in England pursue their course from the point of attachment for several miles without any special topographical episode or change of type—apart from a slight widening here and a narrowing there (Text-fig. 4, p. 79).   Sometimes this condition persists to the apex, especially in the case of banks still in active growth like the Aldeburgh bank in Suffolk.   More usually, however, the apex shows a marked landward deflection, in the form of a *hook*, and frequently several hooks are present in close proximity (Hurst Castle, Hamstead Dover, Text-fig. 4), whilst occasionally extremely complex hook-systems occur, as at Blakeney (Text-fig. 3).

The question of the determining cause in hook-formation is not without interest, and as it has been recently raised by Mr. R. Speight in a joint paper with Messrs. Cockayne and Laing in connection with the two shingle spits occurring in Lake Heron, New Zealand, some reference may be made to the matter.[1]

The causation of hooks, according to G. K. Gilbert, depends upon a temporary change in direction of current, combined with adequate wave-action, or to the spit becoming " at a certain stage of its growth especially subject to some conflicting current, so that its normal growth ceases, and all the shore-drift transported along it goes to the construction of the branch."

" The currents efficient in the formation of a hook do not co-operate simultaneously, but exercise their functions in alternation. The one . . . . . . brings the shore-drift to the angle and accumulates it there ; the other . . . . demolishes the new structure and redeposits the material upon the other limb of the hook." [2]

In accounting for the Lake Heron hooks Speight emphasizes the importance of wave-action, relegating the action of currents to an insignificant place.   He conceives the hook to be formed by the swinging round of the waves in consequence of differential retardation due to the friction of the shelving bottom.   " Both these spits end in a rounded nose " (*i.e.*, hook) " whose position is determined by the amount of retardation of the wave in the shallow water. The wave will tend to swing round completely, so that it actually reverses its direction, and this will maintain a blunt-nosed spit in a fixed position as long as the conditions of the bottom of the lake in the vicinity are the same.   If the floor of the lake keeps on shallowing off the spit so that it makes the depth of the lake more uniform, then the wave will not swing so quickly, and the spit will thus be lengthened."

As a contribution to a discussion on a subject which from the nature of the case probably comes but rarely under direct observation (*i.e.*, the formation of a hook), the following unchronicled incident may be allowed a place.   Had it been a fall of chalk of equal volume at Dover cliffs the occurrence would have been recorded in a hundred newspapers !

At Blakeney Point, as already noticed, the hook-systems reach

[1] R. Speight, L. Cockayne, and R. M. Laing.   The Mount Arrow-
    smith District, a Study in Physiography and Plant Ecology.
    Trans. New Zealand Inst., Vol. XXIII., 1910.

[2] G. K. Gilbert.   Lake Bonneville, U.S. Geol. Survey Monograph,
    1890, p. 52.   Also Rep. U.S. Geol. Survey, 1883-4, p. 95.

a high degree of complexity. One of these hooks (marked by an arrow, just above the letter S of salt-marsh, in Text-fig. 3, p. 78) has in recent years become somewhat exposed to gales from the north-west in consequence of the wasting of the tip of the main bank which formerly masked it. Last Easter (1911), when I was visiting the spot, a succession of heavy gales from this quarter removed the terminal portion of this hook and deposited the eroded material as a new bank, 140 ft. long, 50 ft. wide and over 6 ft. high, at right angles to the old hook on its lee side. The photograph (Pl. 4, Fig. 2) shows the new hook lying at right angles to the old bank (which is seen on the right of the picture with vegetation zones)—the displaced tip of which it represents—as seen from the inside; the same relation is also indicated on the sketch map (Text-fig. 3).
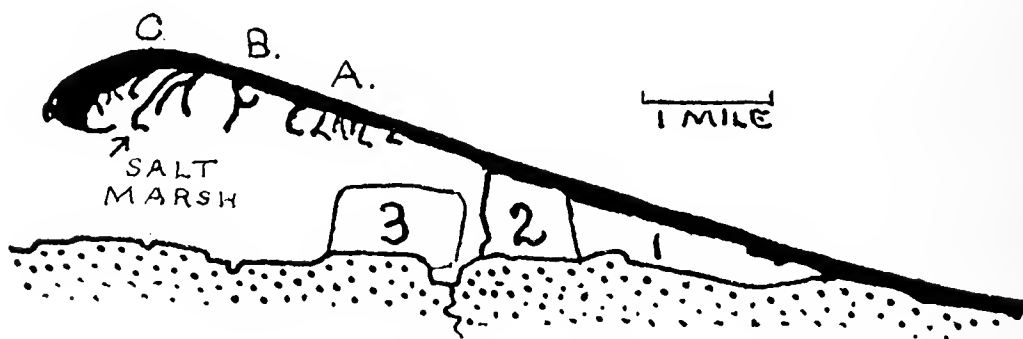
Fig. 3. Sketch map of the Blakeney Bank showing systems of hooks at A, B and C. 1, 2, and 3 denote areas of marshes in the order in which they were reclaimed. The arrow above the letter S in " salt " indicates the position of the bank whose tip was turned at a right-angle in 1911.

The observation tends to support the general position of Speight in so far as it emphasizes the importance of wave-action; at the same time it does not prove that currents have not a part to play. In point of fact, a brisk current runs at this spot at a certain stage of the tide, so that it is impossible to maintain that the organised redistribution of material which has taken place could have been carried out in its absence. At the same time it is obvious that the current alone, so long as the point of this bank occupied a sheltered position, was not efficient to displace the material. It was only when reinforced by appropriate wave-action that this became possible.

The occurrence is also instructive in providing the solution of a structural peculiarity of several of the old hooks further east on the same bank. It will be noted that at A, Text-fig. 3, there is a marked tendency for the hooks to show an L-shaped terminus. In view of what has been related, it may be accepted with some

confidence that the same explanation holds here also, *i.e.*, that the right-angled limbs of these hooks. were produced at some remote period by heavy gales blowing from the west.

So far as the majority of our English shingle spits are concerned, as a glance at our charts of a representative selection will show (Text-fig. 4), the tendency to hook-formation is concentrated at the distal extremity.   In several of these banks concerning which historical records are available (*e.g.*, Hurst Castle, Calshot Spit) there has been no advance for centuries, whilst at Blakeney, after a long period of advance, there has in the last fifty years been actual wasting at the tip.
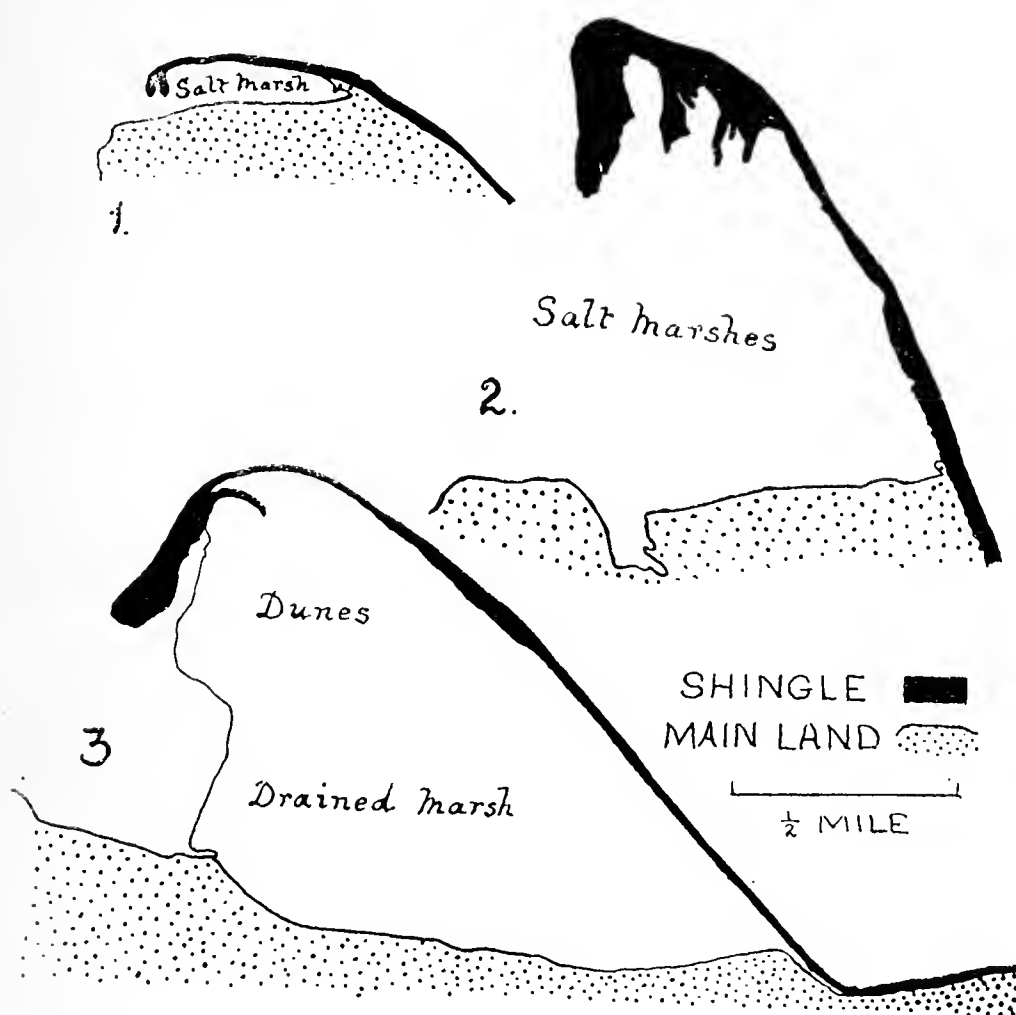
Fig. 4.   Sketch maps of (1) the Hamstead Dover, (2) Hurst Castle, and (3) Northam shingle banks, showing hook-formation.   Maps 1 and 3 have been reversed to facilitate comparison with 2.

In view of this, the conclusion is almost irresistible that a shingle spit has quite definite, successive phases.   There is the phase of youth in which growth is mainly in length ; and this is followed by

a more or less prolonged phase of hook-formation—the phase of maturity. In other words, the spit grows at first under the organising influence of the littoral current, but sooner or later its point will extend to a region where it becomes subject to a conflicting current, so that hook-formation supervenes.

This conflicting current will in most cases be the tidal current which fills the area on the lee side of the spit, and its action in determining hook-formation is automatic—the inevitable consequence of the increasing scour to which the point of a lengthening spit becomes subject. In illustration we may take the case of a spit making an angle of $45°$ with the shore-line. Let perpendiculars be erected on the spit at intervals of a mile and produced till they intersect the shore-line. The area enclosed by the perpendicular at the 1 mile station will be ·5 square miles, at the 2 mile station 2 square miles, at the 4 mile station 8 square miles, at the 6 mile station 18 square miles, and so on. In other words the areas to be filled by the tide mount as the squares of the distances. Thus the volume of water that will have to pass behind a 10 mile spit will be one hundred times as great as that behind a 1 mile spit, and this of course in the same period of time. If the whole of this water were to run in a channel whose sectional area remained constant, the rate of flow in the former case should be one hundred times as fast as in the latter. Allowance has to be made however for progressive shallowing by silting up behind the spit (and consequent relative diminution of the volume of water needed to fill it), and also for the widening of the aperture as the point of the spit gets further from the land. Though it is impossible to attach concrete values to such factors as these, the general conclusion may be drawn with little risk of error that as a spit lengthens it becomes subject to increasing tidal scour, which, when correlated with heavy on-shore gales, will lead to the transfer of material and the production of a landward hook. That hooks are directed towards the land and not towards the sea—notwithstanding the equivalence between the tidal currents of ebb and flow—depends on the non-production of waves when the wind blows off-shore.

Thus we see that as a spit grows in length it will become more and more susceptible to the hook-forming agencies which will also, automatically, arrest its power of growth in length.

There is, of course, another factor which must work in the same sense, *viz.*, the attrition factor. If the supplies of drifting shingle be assumed to remain constant, as the spit grows the losses due to
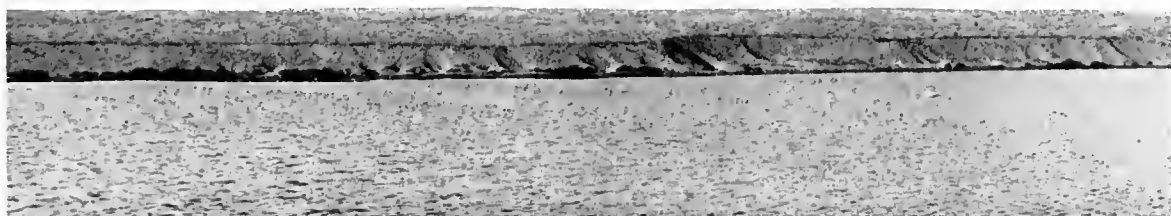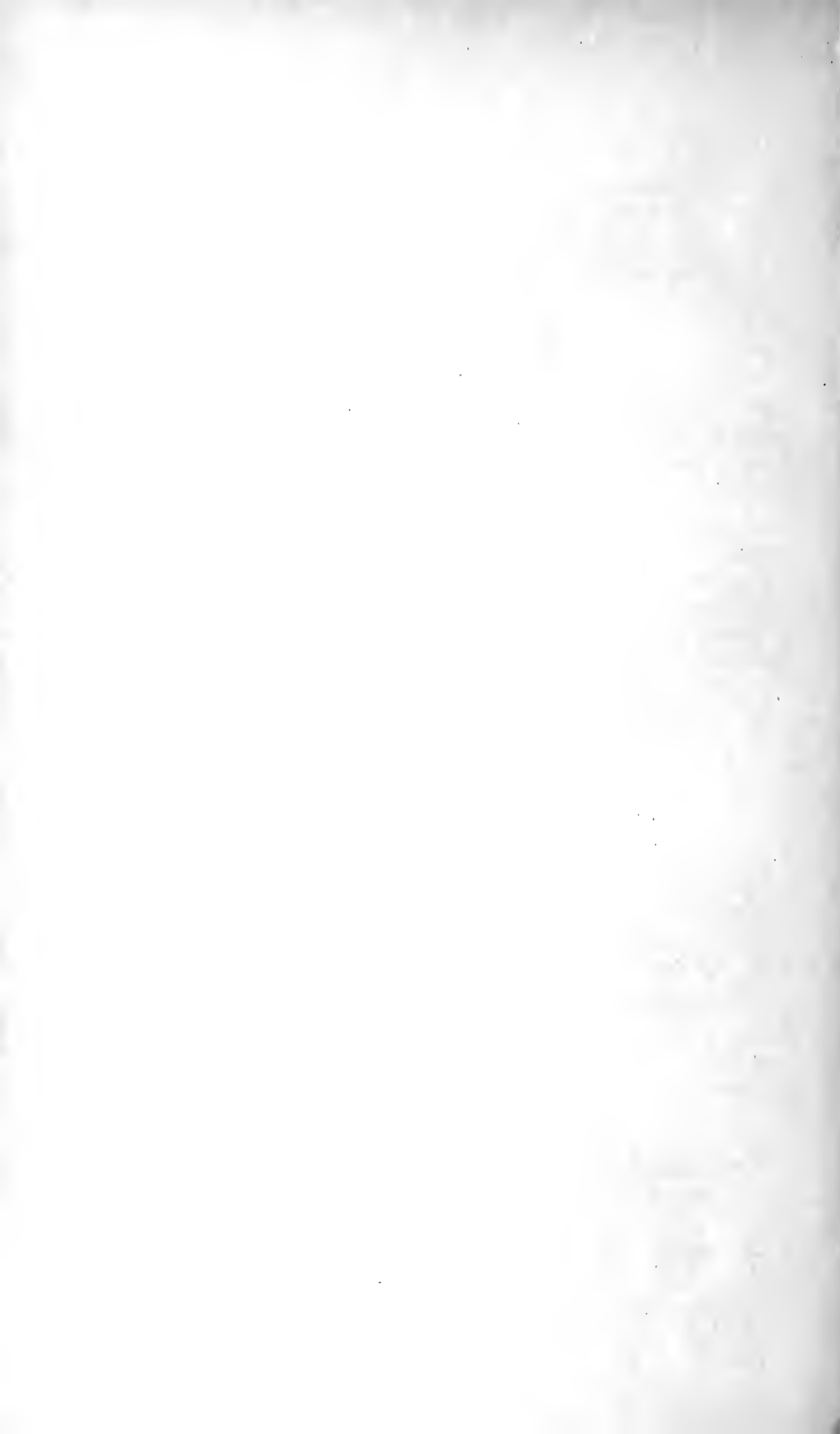
attrition of the travelling shingle will increase—a fact finding frequent expression in the progressive diminution in size of the pebbles as the apex is approached. In the absence of quantitative data bearing on the "life" of the various ingredients of beach material, no quantitative value can be assigned to this factor.

CURVATURE OF SPIT.

Though hooks do not tend to arise, at any rate as normal features, till a spit is approaching the close of its phase of longitudinal extension, there is another characteristic of maritime spits that is probably related to tidal causes. Shingle spits show a distinct tendency towards curvature, and when this is the case the *convexity* is directed to the sea. In the case of lake-shore spits Gilbert remarks that the spit, when not straight, presents its *concavity* towards the lake.[1] If this difference in the sense of the direction of curvature be really of diagnostic value, it is reasonable to suppose that it depends in some way or another upon the tidal currents which form the outstanding feature that differentiates the agencies at work on the sea-coast and lake-shore, respectively. The influence of the tidal current may directly determine the contour of the spit, or it may act indirectly by modifying the littoral shelf on which the spit rests and so determine its form. The matter is an intricate one however, and no useful purpose would be served by discussing it further.

MULTIPLE HOOK-FORMATION.

There are several features associated with hook-formation to which attention may now be directed. Not infrequently a succession of hooks is formed (*e.g.*, Hurst Castle, Hamstead Dover, Text-fig. 4). Often these hooks are so closely approximated that the system which they form essentially resembles the apposition type of bank-building shown at Dungeness (Text-fig. 1). Nowhere is this approximation better illustrated than in the terminal series of hooks at Blakeney Point (Text-fig 3, C), where their numbers can hardly be determined by mere inspection on account of the dunes which mask them.

Noteworthy too is the reversion to the juvenile, straight-growing phase which is occasionally found. This exceptional condition is illustrated on the grand scale by the Blakeney bank, which bears on its distal stretch of two miles no fewer than three distinct groups or systems of hooks—the intervening regions being of the type of the

[1] G. K. Gilbert, Lake Bonneville, p. 52.

straight shingle spit.   The three hook-systems are marked on the map (Text-fig. 3) as A, B and C.   The system A (known locally as " the Marams ") begins about four-and-a-half miles from the point at which the bank leaves the shore, and includes no fewer than eight successive hooks distributed over a length of less than a mile : in association with these hooks, in the bays between, salt-marshes have sprung up.

The group B is one-third of a mile further on, and consists of three banks which have become partially overlaid with blown sand. This system is known as " the Hood."   A quarter of a mile beyond, the last series (C), constituting Blakeney Point, is reached, where at least ten more hooks are involved.

This marked and unusual oscillation of type on the Blakeney Bank suggests the possibility that its explanation is to be found in the special circumstances of the history of this area.   Though it is premature to dogmatise on an obscure question of this kind, it is significant that considerable and successive reclamations of salt-marsh have been carried out on the landward side of the Blakeney Bank (see Text-fig. 3, the areas 1, 2, 3, reclaimed in this order).   It seems obvious that as a consequence of each reclamation less tidal water would be required to fill the marsh, so that the rate of flow and consequent scour at the tip would thus be reduced.   Under these conditions the bank might revert for a while to the juvenile phase, until its extension once more induced an increased scour with further formation of hooks.

However this may be—and the lapse of time since these occurrences makes it improbable that the detailed history of this particular bank should be recoverable—it is quite evident that the formative agencies which co-operate in the building of a shingle spit collectively form a piece of mechanism of extreme sentiveness, liable to respond in a very conspicuous way to any disturbance in the balance of forces which for the moment determine the mode of growth.

Though in the foregoing section the main types of shingle bank have been discriminated, it is expedient to give a brief explanation of the status of the Chesil Bank in relation to those types—more especially as some account of its surface relief and plant habitats will be included in the sequel.

The Chesil Bank forms the most considerable and imposing accumulation of shingle in the British Isles and is more than fifteen miles in length—stretching as a continuous strip of shingle from

Burton Bradstock at the western extremity to Portland at the east. The height of its crest above high-water mark ranges from 20 to 30 feet, whilst its width averages 500 feet. The general features of its structure formed the subject of a well-known paper by the late Sir John Coode,[1] whilst from time to time the questions of the origin and drift of the shingle have been the subject of considerable controversy, and, indeed, are still unsettled.

From Burton Bradstock to Abbotsbury (6 miles) the Chesil fringes the mainland (Pl. 4, Fig. 4); from this point to Portland the bank is separated from the mainland by a shallow estuary, the Fleet or Backwater, about eight miles long and rarely exceeding half a mile in width.
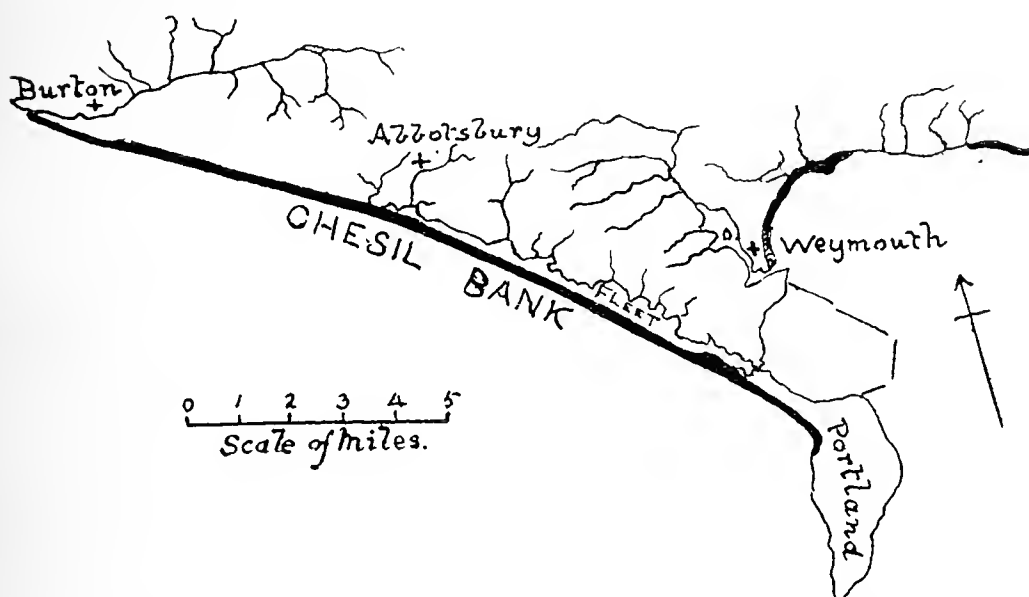
Fig. 5. Sketch map of the Chesil Bank (after Bristowe and Whitaker) to show the relations of Bank, Mainland and Fleet. Shingle is drawn thick black.

In effect, this portion of the Chesil Bank resembles the variety of shingle spit termed a *Bar* (cf. p 74), *i.e.*, that type in which the apex of the spit comes to rest against the land—in this case the island of Portland (Text-fig. 5). It exhibits also many of the phenomena characteristic of shingle spits. Whilst it is possible that the Chesil Bank may in its manner of origin actually be a Bar, there is another view of its nature which has received increasing support in recent times. On this view the Chesil is regarded, developmentally, not as a spit, but as a fringing beach behind which the land has retreated in consequence of sub-aërial denudation. According to this theory—originally formulated by Bristowe and Whitaker[2]—the Fleet or Backwater has been excavated behind the

[1] Proc. Inst. Civil Engineers, Vol. XII., 1853, p. 520.

[2] Geol. Mag., Vol. VI., 1869, p. 433.

bank " as a result of the eastward deflection by the bank of the streams which descend to the shore eastward of Abbotsbury " (cf. Text-fig. 5). This theory finds an able exponent in Mr. Aubrey Strahan, whose evidence before the Royal Commission on Coast Erosion should be consulted on the matter.[1]

Though it is superfluous to recapitulate the facts on which this view is founded, there is one feature pointing in the same direction which has not perhaps been adequately emphasized. The curvature of the Chesil presents its concavity to the sea, and in this seems inconsistent with a spit type of development.

If we assume the truth of this theory, which is certainly attractive, the Fleet or lagoon behind the Chesil Bank, though not *ontogenetically* the equivalent of the salt-marshes which usually lie on the protected side of a shingle spit, may nevertheless be regarded as playing the *same functional rôle*—a point which will be elaborated in further detail.

On the Mobility of Shingle Banks.

It is not proposed here to consider the mobility of shingle in general or the phenomena and laws of its drift below tide-marks. To a botanist legitimate interest only begins when the shingle has been thrown up high and dry to form a habitat capable of invasion by plants. The height to which shingle is raised doubtless depends upon a combination of factors of which the chief are the height and velocity of storm-waves and the presence or absence of deep water at the foot of the bank. The crest of the Chesil Bank has a S.W. exposure and rises out of deep water twenty to twenty-five feet above the high-water mark of ordinary spring tides; that of the Blakeney Bank with a northerly exposure and shoaling shore, six or seven feet; whilst the Hamstead Dover, in the protected waters of the Solent, rises no more than a bare two feet. But when the shingle has reached the crest it finds no permanent place of rest, except in banks of the apposition type, where a newer ridge will be thrown up, isolating the last from the influence of the surf.

So long as the sea beats on a shingle bank, so long will its component parts be liable to motion, unless it be covered and protected by dunes or—what very rarely happens in Nature—becomes so densely clothed and bound with a robust vegetation as to defy the violence of the elements.[2]

[1] Minutes of Evidence, Royal Com. on Coast Erosion, Vol. I, pt. 2, 1907, esp. answers Nos. 3624-3718, pp. 133-136.

[2] The Calshot Spit bears dense mixed scrub and a few trees.

There are three principal ways, quite distinct from one another, in which shingle is kept mobile; though all are operative on nearly every bank, their relative importance will vary in different cases.

A.—WAVE IMPACT.

.The first of these methods comes into play under the influence of the more violent on-shore gales, and consists of the scattering of the shingle over the back of the bank as the waves break over the crest. In this way shingle already in place is kept on the move, whilst new shingle is contributed from the tideway. Its results are manifest on the Blakeney Bank in the finger-like points of shingle which stretch out over the marshes on the leeward side at numerous places (cf. Pl. 4, Fig. 3).

The same phenomenon is unusually well shown on parts of the Hamstead Dover—a shingle spit of small dimensions on which mobility-effects, in addition to other features, are displayed under exceptionally favourable conditions for study. Here the spit is flanked on the landward side by a series of pointed tongues of shingle which lie diagrammatically in the direction of principal wave-impact. The cumulative effect of these displacements is very manifest on this spit, as the parts most subject to this buffeting show a distinct landward sag (just visible on the chart, Text-fig. 4).

The evidence of direct wave-action, so manifest on these and other banks, fully confirms local testimony that when a heavy on-shore gale coincides with a high spring tide, the crest and back of the Blakeney Bank are awash. Under these conditions the whole structure must be so permeated with water as to render the shingle practically fluid.

Mobility induced by wave-impact will in the long run bring about a landward creep of the bank—not equally everywhere, but now here, now there. The statement occurs in one of the Reports of the Coast Erosion Commission[1] that the Blakeney Bank is drifting landwards at the rate of two yards a year. Though the precise data on which this estimate is based are not cited, I can well believe it to be no exaggeration.

An outstanding example of this type of mobility is the Northam pebble ridge which defends the famous golf course of Westward Ho! against the sea. The matter has reached a critical phase in recent times, and is now causing serious local anxiety. Whilst moderate wave-impact tends to the maintenance of the crest at a

[1] Roy. Com. on Coast Erosion, Min. of Evidence, Vol. I, pt. 2, appendix XXIII, p. 240, 1907.

proper height, if it be excessive the result is to drive the shingle over the marshes and at the same time to reduce the height of the crest.

B.—PERCOLATION.

With the above is to be contrasted the landward displacement of shingle as a consequence of percolation. As a result of its open texture, shingle is readily traversed by water. On the Blakeney Bank towards the time of high tide, when the sea level outside is well above that on the marshes, and especially when a heavy sea is running, sea-water normally traverses the bank, breaking out on the lee side just above the level of the saltings in numberless springs. This phenomenon is accompanied by the displacement of a certain amount of shingle, but, regarded as a factor in the general landward creep of the bank as a whole, this displacement is relatively unimportant, owing to the small height of the bank above high water.

In cases, however, like the Chesil, where the bank rises to a height of 20 feet or more above tidal limits, and usually at a steep angle which often approaches the critical angle of rest of the component materials, the results of percolation are both striking and important.

If the Chesil Bank be viewed from the mainland at, e.g., a point east of Abbotsbury, its landward or N.E. face appears as a cliff scored by a series of deep ravines. Our photograph (Pl. 4, fig. 1) provides such a view taken from the foot of Chesters Hill, two miles east of Abbotsbury. Over the Fleet, here about 400 yards in breadth, the bank rises from a low terrace which is fringed along the water's edge by a line of bushes of *Suæda fruticosa* (conspicuous in the photograph). This terrace, foreshortened in the picture, is just above the water-level and has an average width of about 70 feet. The slope of the bank from the terrace is steep for the first ten or twelve feet; the gradient then becoming more gentle as the summit ridge or crest is approached.

At the back of the terrace the foot of the slope is carved into a series of deep ravines which reach a height of 10—12 feet, and with the intervening buttresses form the conspicuous relief of the photograph. The back and sides of the ravines are formed of bare shingle inclined at the angle of repose (about 34°); bare shingle likewise forms the floor which is generally scored by a low gully connecting with a detrital fan of shingle projecting out into the Fleet some eight or ten feet beyond the edge of the terrace.

Between the ravines, which in some places are very close together, in others more remote, are buttresses of shingle in a quiescent state and bearing a sparse vegetation. The faces of these buttresses are inclined at a lower angle than the sides of the ravines and they merge above without material change of slope in the sloping back of the bank.

The accompanying sketch (text-fig. 6) for which I am indebted to my friend Mr. T. G. Hill, gives a good idea of the detailed relief
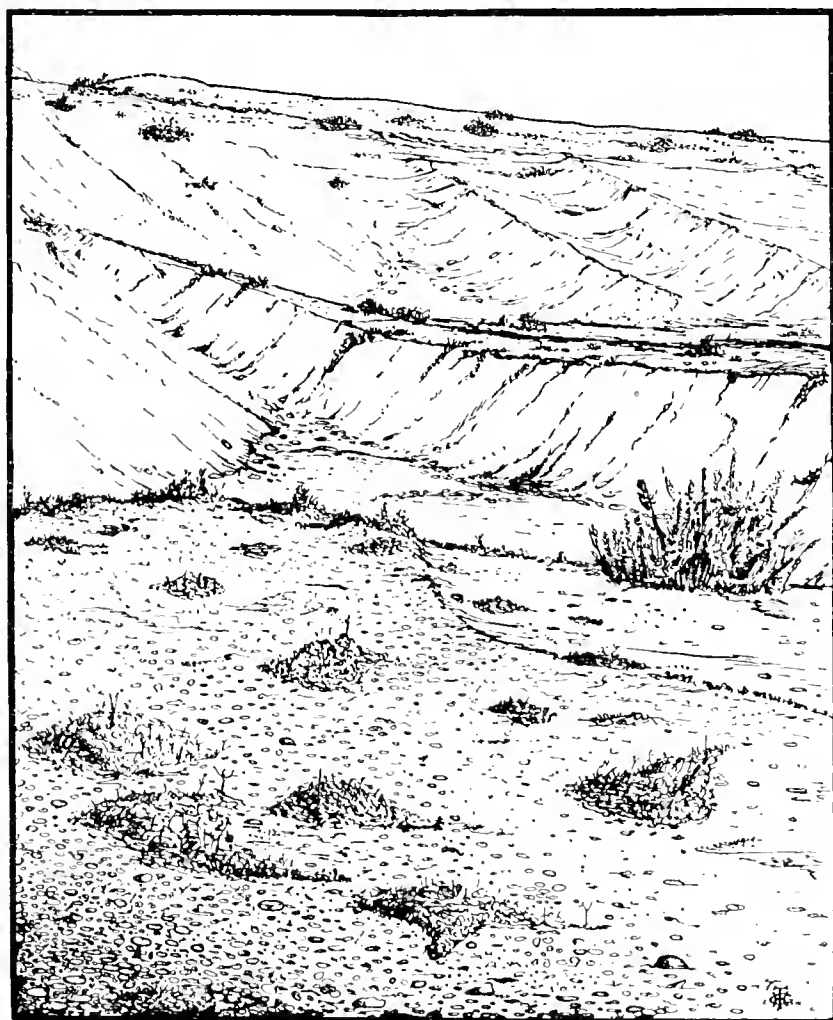
Fig. 6. Shingle ravines on the Chesil Bank as seen from the Terrace. Sketch by Mr. T. G. Hill.

of these ravines. It is taken from the foot of a buttress where it joins the terrace. The sides and floor of the nearest ravine are bare of plants except for the solitary bush of *Suæda fruticosa* around which shingle is being thrown. The flat top of the buttress (above the bush) bears scattered plants of *Silene maritima*, whilst beyond this is a succession of other ravines and buttresses. The water's edge is outside the picture to the right, about twenty feet

away, whilst the sky-line is formed by the higher slopes of the bank. Beyond the sky-line is the crest, from which the bank drops abruptly to the sea.

The mechanism by which these ravines are carved and shingle dislodged and shot out to form fans projecting from the terrace is percolation by the sea. At high tide and especially with heavy on-shore gales, sea-water runs through the bank like a sieve, gushing forth at many places at the foot of the landward slope. At the points where the water flows out, shingle is displaced, and this causes the shingle above to be dislodged and slide down its " slope of repose." In this way the ravines are usually cut deeper and deeper into the bank, the dislodged material being vomited forth by the gully on the floor as detrital fans.

The efficiency of this mechanism will depend on the height of the breaking waves on the sea front above the water-level of the Fleet. The latter—which shows little oscillation—is about 4 feet below ordinary high-water-mark outside. As a consequence, percolation takes place in both directions, *i.e.*, from the sea into the Fleet when the waves are breaking at a high level, and at low water a gentle percolation in the opposite direction—indicated by a reversed flow in the gullies or channels on the floor of the ravines.

In the absence of systematic records it is impossible to make any quantitative estimate of the amount of shingle that is shifted by the operation of this process; but that the amount is large and the result important in relation to the vegetation is evident from an inspection of the ground.

It will be understood that the result of the operation just described is the transport of shingle from the higher parts of the bank on to the terrace below, and especially the projection of this detritus in the form of fan-like platforms beyond the general edge (the dotted line in Text-fig. 7, a section of the bank, illustrates the nature of this transfer). By this means the terrace advances landwards at the expense of material derived from the higher slopes. Though it is not possible to say for how long a time a given ravine remains in the active phase, it is manifest that this activity is intermittent and that ravines go out of action and remain quiescent, probably for years.

Terrace formation by ravine-agency is of course only one part, and a minor part, of the big phenomenon of landward creep which is always in progress. That the latter is possible depends primarily on the constructive action of the waves, which pile up the shingle

on the crest and scatter it over the back, thus maintaining the heighth of the bank. These two processes, the one anabolic, the other katabolic, are doubtless closely related; and, taking the bank as a whole, their combined action must be fairly evenly distributed along its length, since the course of the bank from Abbotsbury to Portland follows a very even curve—though in detail, slight inequalities, not indicated in the higher scale maps, are discernible to the practiced eye. It is probable that these inequalities which exist on the seaward face would, if carefully correlated with the regions of activity and repose on the lee side of the bank, fully repay investigation.
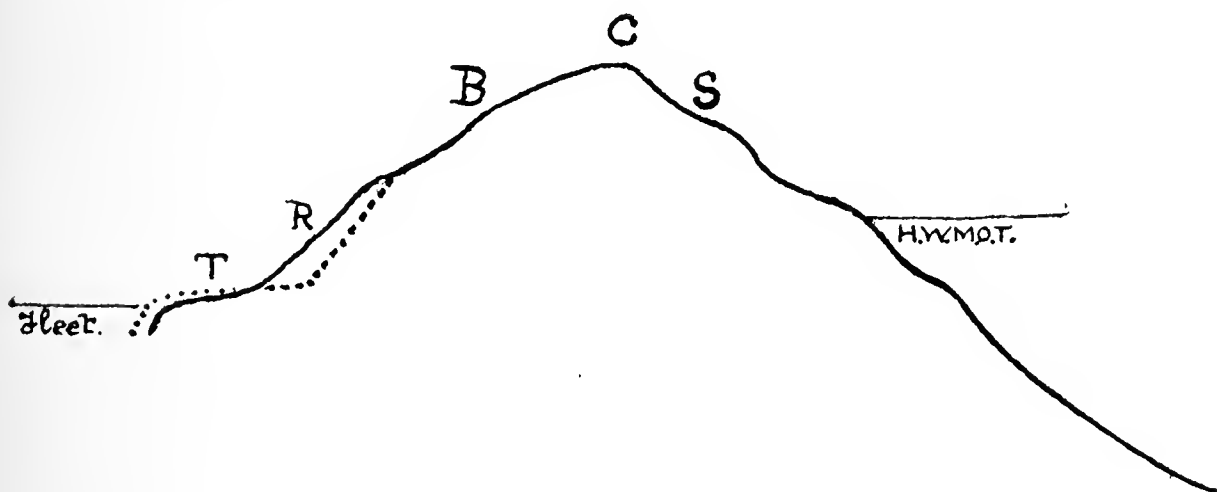
Fig. 7. Profile of the Chesil Bank east of its point of separation from the land. The dotted line is to show the cutting back of a ravine and the transfer of the talus to the terrace. S., Storm Shelf; C., Crest; B., Back; R., Ravine; T., Terrace; H.W.M.O.T., High Water Mark Ordinary Tides. The vertical scale is much exaggerated.

To recapitulate*: so far as observation goes there can be little doubt that the Chesil Bank as a whole is creeping slowly shoreward, the onshore gales piling the shingle up, whilst, as a result of percolation, it makes its way down on to the terrace, which is continually advancing, now here, now there, across the Fleet, but on the whole with remarkable evenness.

C.—UNDERCUTTING.

Though of little moment in renewing the surface of the shingle, a third method merits passing reference, *viz.*, the mobility which arises from undercutting on the lee side by tidal or other currents. In this way a talus is sometimes kept active for an indefinite period, as for instance on the Blakeney Bank at the point where the channel of the River Glaven (near Cley) impinges on the Bank. In some

cases it seems probable that this form of erosion may play an important part in regulating the landward creep of a bank. If the view be accepted that the Fleet has been carved out behind the Chesil Bank by the deflection of a number of small rivers (pp. 83–4) it can hardly be denied that the same forces which have assisted in the wasting of the shore line would also have become operative in retarding any local tendency that might be shown by the bank itself to advance, and by so doing restrict the channel of the Fleet. In this way we get perhaps a glimpse of one of the factors which, operating automatically, wherever it is required, has been able to maintain unimpaired the outstanding peculiarity of the Chesil Bank, *viz.*, the marvellous alignment of all the parts throughout its length.

THE RELATION OF THE MAIN SPIT TO THE HOOKS.

An obvious consequence of the shoreward movement of a bank provided with lateral hooks is the overwhelming or enclosure of the proximal parts of the hooks as the encroaching edge of the mobile main bank advances. That this result does in fact occur is manifest to any passer-by who cares to examine the series of hooks at the " Marams " on the Blakeney Bank. The phenomenon of " hook-slide," however, claims the attention of the botanist on account of the reactions which the vegetation exhibits in relation to it.

It will be readily appreciated that so long as a hook (such as 3 in Text-fig. 8) remains terminal in position and is directly exposed to the surf, so long will it, like the rest of the main bank, be kept in a continuous or intermittent state of mobility. When, however, by the further growth in length of the main bank the position of the hook ceases to be terminal (as in 2 or 1, Text-fig. 8) and its flanks are washed only by the protected and relatively quiet waters of the estuary, the hook enters on a long phase of dormancy.

This phase of rest, wherever it has been studied (Blakeney, Hurst Castle, Hamstead Dover), finds expression in an altered vegetation or " succession " which contrasts strikingly with the pioneer vegetation of the main bank. New plants not found on the main bank make their appearance, whilst others characteristic of the main bank no longer occur. There is, however, a residuum of plants common to the two types of habitat.

The main bank slowly driven shorewards encroaches not only on the marshes but also on the hooks, embedding them as the main trunk of a thickening dicotyledonous tree embeds its branches

(diagrammatically illustrated in Text-fig. 8). Across the proximal
ends of many of the hooks of the Blakeney " Marams " a low talus
of mobile shingle is present, and *pari passu* with its advance the
plant succession becomes retrogressive, in the sense that many of
the plants of the dormant hook are unable to colonise the new
(mobile) surface, whilst others belonging to the pioneer vegetation
of the main bank reappear.
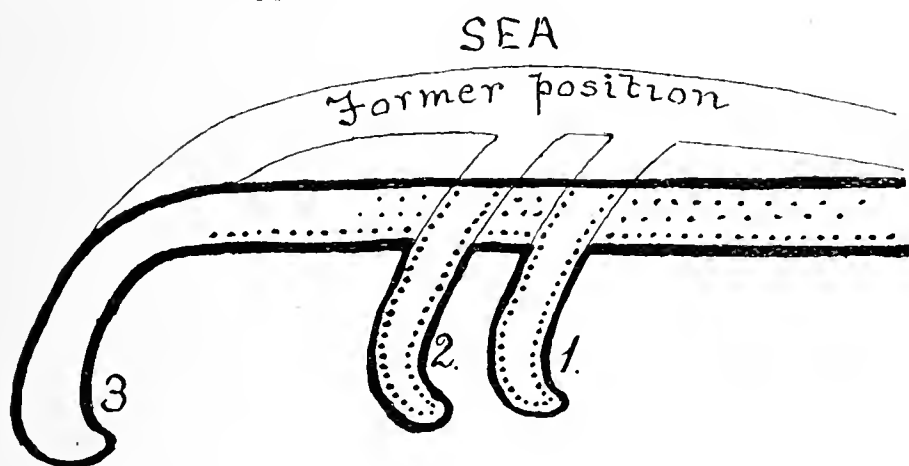
Fig. 8. To illustrate "hook-sliding." The heavy outline represents the
present position of a bank with three hooks. No. 3 is terminal, Nos. 2 and 1
lateral in position. The former positions of main spit and the proximal parts
of the hooks are indicated by the thin outline. The dots show the distribution
of *Suæda fruticosa*.

Among the plants common to the main bank and hooks at
Blakeney is *Suæda fruticosa* (Pl. 4, fig. 3). *On the main bank* this
plant establishes itself from drift-borne seed in great numbers on
the inner fringe of shingle bordering the salt-marshes. As it
tolerates the heaping up of shingle over its roots this plant tends to
survive the advance of the shingle and to remain growing at various
heights on the bank in positions to which it has ascended much as
do Psamma or Salix under analogous conditions on a wandering
sand-dune. Thus we find *Suæda fruticosa* both on the fringe (the
place of establishment) and on the body of the main bank. *On the
hooks* this plant clothes the slopes on both sides but is absent from
the top. At the place of junction of hook and main bank the fringe
of Suæda is of course interrupted along the latter (Text-fig. 8;
Suæda plants represented by dots).

If now, as indicated by the evidence, the main bank is creeping
landwards over marshes and hooks alike, it is to be expected that
the distribution of the Suædas on the main bank will be in conformity
with the two sources from which they are derived, *i.e.* (1) the plants
that establish themselves on the fringe, (2) those on the flanks of
the hooks. Careful inspection of the ground shows that this

probability is realised on the " Marams " at Blakeney, for in several cases those parts of the main bank which are in alignment with the proximal segments of the hooks are free from Suædas except for a double row (corresponding with the flanking rows of the hooks) running obliquely up the bank (Text-fig. 8). On other parts of the main bank no such restriction in the distribution of the Suæda is found to occur.[1]

In view of these results, inferred from the vegetation, it seems likely that the hooks on the " Marams " were formerly considerably longer than is now the case. The main bank is slowly creeping over them, and their proximal ends have doubtless long ago emerged on the sea face and been disintegrated by the waves—an inference susceptible of corroboration by a direct search for old surfaces by probing or digging. This bit of vanished history is reconstructed in Text-fig. 8 ; former contours being sketched in thin lines.

The phenomena associated with " hook-sliding " have a general as well as a merely particular interest connected with the history of the Blakeney Bank. They serve to emphasize the importance of the historic treatment of a vegetation—of the detailed study of the ontogeny and " succession " of a vegetation in determining the status of its component elements.

The Various Types of Habitat.

It will have been gathered from the preceding account that a shingle spit should show a considerable diversity of plant habitats in respect of both exposure and mobility ; an expectation at once confirmed when the ground is inspected—not only in respect of the two factors named, but also in the nature of the soil which occupies the interstices of the coarser materials.

First, the principal topographical regions must be enumerated and provisional names allotted for convenience of reference.

The primary regions will include (1) the main bank, and (2)

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[1] The tenacity with which *Suæda fruticosa* holds its own on the Blakeney Bank regardless of the mobility of the shingle is certainly worthy of record. Under the milder climatic conditions of the Chesil Bank this plant is restricted to the terrace and appears to be incapable of rising more than two feet at the outside when the shingle collects above it. At Blakeney, on the other hand, Suæda is found all over the bank, persisting even to the crest, seven feet above spring tide high-water-mark, and occasionally in isolated specimens a little distance down the sea face. This difference in behaviour at the two localities is hardly to be explained on climatic grounds—more probably it is determined by the composition of the soil.

the hooks. The former are of course largely mobile, the latter quiescent.

The *Main Bank* in practically all cases exhibits many features in common. It has a sea face and a land face separated by the *Crest* (Text-fig. 7, C) ; the sea face as a rule is the steeper of the two faces, and rises in a series of more or less well-marked steps or platforms corresponding with the various categories of tide-marks. Apart from the topmost of these platforms (not reached by ordinary tides) which may be termed the *storm shelf* (S), the rest of this face bears no vegetation on account of its mobility. The vegetation of the storm shelf is usually very sparse indeed, and largely consists, when present, of prostrate species of *Atriplex* and sometimes *Beta maritima.*   The plants of the actual crest have much in common with those of the storm shelf, and it is evident that exposure to the winds (and doubtless spray) presents a serious check to plant establishment in either position.   The crest is sometimes distinguished, as at Blakeney, by being the last strong-hold of several plants endowed with the capacity of creeping up the shingle from the landward side (cf. p. 92, footnote), but they are the merest vestiges of their former selves and shortly succumb.

The *Back* of the bank (B) slopes away from the crest, usually at a low angle ; sometimes, as on the Chesil, the slope may reach 10—15°.   On banks which do not exceed six or eight feet in height above high-water-mark, the bank slopes gradually down to the marshes, but on high banks, like the Chesil, it falls away steeply in a series of *ravines* (R) which give on to the horizontal ground or *Terrace* (T) forming the landward fringe of the bank.   Between the ravines are dormant buttresses, essentially downward continuations of the back, from which they differ in no material respect.

The back is the principal region of vegetation and it is here that the greater number of " shingle plants " occur.   In respect of mobility a wide range is shown, and to some extent the mobile and resting parts are distinguished by their vegetations.   Perhaps the crustaceous lichens are to be reckoned the most sensitive indicators of dormancy, though their behaviour on different banks stands in need of elucidation.   Thus, whilst on the main bank at Blakeney lichens are hardly met with at all, on the Chesil extensive areas become covered with lichens and it is evident their settlement is quickly accomplished as soon as the conditions become favourable. Difference in climate may account for much, but the question needs comparative experimental investigation before it will be possible to

attach any quantitative (time) significance to the presence of a given lichen on a stone. From this point of view the lichens of the shingle bank are an untouched and highly promising field.

Good indicator-plants are also provided by the Angiosperms : thus *Geranium robertianum* v. *purpureum* belongs essentially to dormant areas, whilst *Lathyrus maritimus* at its best is indicative of the unstable condition.[1]

The *terrace* or fringe is the great gathering ground of the halophytic plants—escapes from the salt-marsh. Other plants are those common to the back, especially on the dormant parts. Matricarias perhaps are characteristic. Lichens occur in great profusion and luxuriance, and include Cladonias and other fruticose and foliose forms. On the mobile places (detrital fans) *Suæda fruticosa* breeds and establishes itself : elsewhere it merely survives. This plant is the chief glory of those banks on which it occurs and offers many problems requiring explanation (cf. p. 92, footnote).

Climatically, the terrace is warm and sheltered, in marked contrast with the crest. In summer, on a high bank like the Chesil, it is sheltered to the point of stifling. When investigated, doubtless the climatic factor (in the wide sense) will prove to be important on shingle banks and may well be correlated with plant-zonation.

The *Hooks*—apart from the terminal hook—are notably passive and consolidated, and never fail to show a "succession." Among their distinctive plants may be mentioned *Inula crithmoides* (Hurst Castle, Hamstead Dover) and *Limonium binervosum* (Blakeney). The flanks of the hooks are under tidal influence and show a striking zonation in which the halophytes are conspicuous, whilst the flat summits bear a closed grassy "gravel association." As the shingle of the main bank advances over the hooks the vegetation of the latter reverts to the pioneer type.

Shingle Banks of the *apposition type* show very distinctive features dependent on their isolation from the sea. This affects them in three distinct ways. They are essentially dormant ; they lack the humous materials left by the tidal drift on other banks ; and they are denied the accession of seeds and other propagula in which the drift abounds.

Consequently these vast areas of shingle (Dungeness, Rye) tend to remain long sterile. In the neighbourhood of habitations and traffic many ruderal plants establish themselves, and sometimes

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[1] No doubt when "mobility" is more fully analysed and studied, a distinction based on the plants will be possible, *e.g.* between places of erosion and places of accumulation.

with interesting results. Thus, to the west of the Martello tower at Rye Harbour the Common Stinging Nettle (*Urtica dioica*) has become widely dispersed, and eventually the bare shingle banks are completely transformed into verdant, grassy lawns. The method is as follows. The Nettle establishes itself in a narrow zone at the foot of the bare bank and slowly works its way up to the summit. In its immediate wake a closed association of fine grasses follows, flourishing on the ground prepared for it by the decay of the nettle-rhizomes. The last stage shows the nettles arrived at the top with the grass choking them out. Their work is finished; the only useful work in Nature I ever saw the Nettle perform!

When apposition banks are formed on any considerable scale, they become of course relatively remote from the sea. This probably makes them climatically different from the other types of bank, and taken in conjunction with the undulating nature of their surface, perhaps explains the comparative readiness with which shrubs and even trees spring up upon them. Characteristic of these may be mentioned *Rubus, Ulex europæus, Cratægus* and *Sambucus nigra*.

This brief epitome of shingle habitats will suffice to show that much information has yet to be collected and compared before even a provisional treatment of the vegetation is possible. The more obviously distinct types of habitat in respect of the physical conditions are (1) the crest and storm shelf; (2) the back and buttresses; (3) the terrace (dormant parts); (4) the terrace (mobile parts); (5) the hooks; (6) the apposition banks.

As regards the plants themselves, the question is sometimes raised as to whether there are any real shingle plants apart from the numerous invaders from the salt-marsh, the plants of sandy ground, and the ruderal plants so commonly found.[1] How this may be I hope to consider on a future occasion. It may be remarked, however, that not a few of the apparent anomalies of plant-distribution on shingle banks find their explanation when it is realised that their distribution is determined not by the shingle but by some other factor. The case of *Arenaria peploides* is a good illustration. This plant forms extensive mats over a large part of the back of the Blakeney Bank, though there are certain stretches from which it is conspicuously absent. On the Hurst Castle bank it is very rare, and it thrives badly and only in small quantities on the Calshot Spit. Only a single specimen was detected on the

[1] Cf. A. G. Tansley. "Types of British Vegetation," p. 353.

Hamstead Dover, whilst, so far as has been ascertained, there is only one locality for it on the Chesil Bank between Burton Bradstock and Wyke Regis (twelve miles). Now *Arenaria peploides* is one of the most characteristic of arenicolous plants and I have not the least doubt that its occurrence in all these cases is determined by sand which is present. The apparent anomalies of its distribution are therefore referable to fluctuations in the composition of the beach materials on the various banks. Other examples of the same kind could be cited, but this is not the place for a critical survey.

The Origin of the Soil in Shingle Banks.

Isolated as they are in position and sterile in nature, shingle beaches and especially shingle spits entirely belie their appearance in regard to the soil which they contain. In point of fact the shingle spit is remarkable, if not unique, among plant habitats, for the richness of its outside supplies of humus-forming materials. And, in addition to these it retains, of course, the products of the disintegration of the vegetation which it bears.

The great source of supply is derived from the *drift*, and this for convenience may be divided into that derived (1) from the open sea, (2) from the salt-marshes on the landward side.

The drift from the sea is generally considerable in amount and includes the usual flotsam and jetsam—bits of wood, bark, corks, pine cones, seaweeds, and the like. These are lifted high up by the waves and are scattered by the wind as they dry over the crest and back of the bank. They may be found in all stages of disintegration, and are readily "assimilated" by the open-textured shingle. Of much greater importance, however, is *the drift from the salt-marshes* left by the tides at the foot of the lee slope or on the terrace. The amount of this marsh-drift that becomes available is simply prodigious, and from the nature of the case, none of it is lost. The constant slipping of the shingle on this side of the spit ensures continuous inter-statification of humus and shingle like a sandwich of the " Swiss roll" variety. The process is always at work, and as a result the lower parts of the bank become thoroughly permeated.

The new bank formed at Blakeney Point last Easter was examined from this point of view, and it was surprising to find what immense blankets of drift it had trapped. The horizontal lines of drift, visible in the photograph (Pl. 4, fig. 2), give but an imperfect idea of the richness within. The very storms which built

up the bank also loosened and conveyed the drift to the lee slope, where it became imprisoned by the talus of shingle washed over the crest.

Thus it is evident that the same mechanism which builds up the bank and keeps the shingle mobile, also provides that which is required to give it fertility.

Nor is this all. Drift is not mere organic matter; it is also the great agency by which seeds are brought to the bank—the seeds of the plants which establish themselves there—and it is under its protection that they germinate. From our point of view the drift, therefore, is the all important thing.

The nature of the drift. The components of the drift are recruited from the salt-marshes, and include everything on the marsh or mud flats that the tide can sweep up. Algæ such as *Rhizoclonium* and *Enteromorpha*; the leaves of *Atriplex* (*Obione*) *portulacoides*; the stalks and chaff of *Spartina*; twigs of *Suæda fruticosa*; the dung of rabbits which browse on the marsh; the carcases of small crabs and other animals which perish; and above all in quantity, the rhizomes and leaves of *Zostera*.

Tidal drift provides a field of special study yet to be opened up. The manurial value of various drifts has never been systematically investigated. The seasonal phenomena connected with drift and the relations of drift to the plant and insect-life of the shingle bank, these and other departments of the subject would doubtless reward investigation. At present it is only possible to state the crude fact that the same machinery which organises the spit, provides also the means of its fertility.

To appreciate the significance of the drift it is only necessary to see how those shingle banks fare which are denied contact with tidal waters. Apposition banks are of this order and they are notorious for their enduring sterility. The same result is apt to appear when the salt-marshes under the lee of a shingle spit are dyked off and the tidal waters excluded. The drift no longer circulates and the bank is starved of its lawful food. Nor can the marsh-holders hope indefinitely to continue in the enjoyment of the reclaimed land. The starved portions of the shingle spit will tend to become more and more sterile and proportionately more mobile, and Nemesis will overtake them in the form of excessive encroachment of the shingle on the dyked marshes.

> "He who will not Nature's way,
> Will in good time have to pay."

THE WATER PROBLEM.

One of the outstanding mysteries of the shingle spit is the water relation. The sides of the spit are washed by the sea and the plants of the lowest zone where the saline influence is supreme are halophytic. Higher up the bank, however, the conditions are quite different. A portion of the members of the halophytic zone, as we have seen, make their way up to the higher slopes, but there is a well-marked residuum of shingle plants which behaves as if, and is indeed known to be, intolerant of salt (Na Cl).

In conformity with this distribution, the water in the interstices in the shingle above the true salt zone is largely free from salt. To the taste it is fresh, which means that, at most, only small traces of Na Cl can be present.

Moreover, the water of the shingle is astonishingly copious, and suffers no diminution during periods of prolonged drought. Throughout the past summer, with the longest periods of high evaporation recorded for this country, numerous shingle spits came under observation, and in no instance did the vegetation show any trace of suffering from drought. On the contrary the wetness of of the shingle just below the surface was maintained unimpaired, and this quite irrespective of the presence of humus or other capillary matter in the interstices of the shingle. It is therefore not possible to account for these inexhaustible supplies of water as conserved rainfall.

Late in the summer the mainland by the Chesil Bank became completety parched up, so that not a green blade of grass was to be found. It was under these circumstances (Sept. 25th, 1911), that our photograph Pl. 4, fig. 4) was taken, showing sheep (which had wandered down of their own initiative) grazing on the fresh *Silene maritima* of the shingle at the Burton Bradstock end of the Chesil.

Not far from this locality, on the same occasion, quantities of *Polygonum amphibium* were found to be growing with great luxuriance on the shingle—corroborative evidence, if such be needed, of the high level of the saturation of the ground.

The source of this water is a matter of no little interest. Now in connection with the analogous problem of the presence of permanent moisture near the surface of high sand dunes the suggestion has been made by more than one writer[1] that it depends upon the

[1] A. Jentzsch, in Gerhardt's " Handbuch d. deutschen Dünen-" baues," 1900, p. 104.
P. Olsson-Seffer. " Hydrodynamic Factors influencing Plant-Life on Sandy Sea-shores." NEW PHYT., Vol.. VIII, p. 43, 1909.

formation of internal dew in the soil, though I am unaware whether the question has been experimentally investigated. In the case of the shingle this solution comes first to the mind, and there is considerable reason for believing that it will turn out to be well founded.

In any case it would be a serious error to classify the shingle bank, on grounds of inadequate water supply, with the so-called xerophytic habitats. Shingle plants no doubt on occasion have to suffer vicissitudes, leading to unfavourable conditions for vegetation, but these arise from causes other than a defective water supply.

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EXPLANATION OF PLATE IV,

ILLUSTRATING PROF. OLIVER'S PAPER ON " THE SHINGLE BEACH AS A PLANT HABITAT."

Fig. 1.—Photograph of the landward face of the Chesil Bank seen over the waters of the Fleet or Backwater. Above the line of cliff the sloping bank bears a discontinuous covering, mainly *Silene maritima*. Below this the ravines separated by buttresses. At the water's edge the terrace (foreshortened) fringed with bushes of *Suæda fruticosa*. Photograph taken Sept. 1911, from the foot of Chesters Hill, about two miles east of Abbotsbury.

Fig. 2.—Photograph of new hook at Blakeney Point, formed in March — April, 1911, on the bank marked with an arrow in Text-fig. 3. The stump of the old bank is on the right (with vegetation). The new bank stretches across the picture and rests on the saltings ; it has blocked the outflow of the creek which enters the picture low down on the right. The horizontal streaks on the bare shingle consist of tidal drift. Photograph taken July, 1911, by Mr. E. J. Salisbury.

Fig. 3. Inner edge of Blakeney main shingle bank encroaching on the " Marams " ; looking west. The bushes are *Suæda fruticosa*. The photograph was taken in September, 1908, and the bare projecting fingers of shingle have since that date become partly covered by a growth of seedling Suædas.

Fig. 4. Chesil Bank looking S.E. from a point opposite Burtons Mere, near Burton Bradstock. The grass on the downs is completely parched by the drought, and sheep have come down to graze on the fresh succulent *Silene maritima*, of which considerable quantities are present. Photograph taken September 25th, 1911.

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THE BRITISH VEGETATION COMMITTEE.

THE record of this Committee has from time to time been outlined in these pages. Since the proceedings were last reported (N.P. VIII, p. 203, 1909) meetings have been held in Liverpool, London, Manchester (2) and Aberystwyth, each with satisfactory results as regards attendance and progress. The constitution of the Committee has undergone one fundamental change through the institution of an Associate-membership. This may be described as a matriculation stage open to active workers on vegetation. In the case of younger members, at least, it is inevitable that though for a time they may as research students take up ecological studies, they may later, from inclination or necessity, become no longer active in the field ; during the earlier period it is advantageous to meet other

workers and to become acquainted with methods and outlooks. In practice, the associate-member has at his disposal all the pleasant parts of each meeting—discussions, communications, and excursions,— whereas he has not to endure the necessary and often less interesting " business " unavoidable in any organisation. Through the inclusion of associate-members the Committee has increased in numbers, and the presence of enthusiastic recruits with all the advantages of the more modern ecological outlook in Botany is good for all. On the other hand changes have necessitated the resignation of four members (three of them original) who have now transferred their activities to other branches of work. If the Committee is still to retain its original object—to promote the *active* study of British Vegetation—such partings are inevitable, however much one personally regrets them.

International Phytogeographical Excursion, 1911.

The importance of this event may be summed up in a remark overheard by the writer, that if the Committee had done nothing else its existence would have been justified by the promotion of the Excursion of August, 1911 and the publication of " Types of British Vegetation " as an outcome of the Excursion project. The fact accomplished has been summed up by one veteran foreign member of the party : " our Britannic tour was a splendid success." It is unnecessary here to enter into details, as these have already been given in this journal from the itinerant aspect (N.P., X, pp. 271— 291) and from the aspect of floristic results (N.P., X, pp. 306— 328). The majority of the members of the Committee joined the excursion at one stage or another, and the Committee as a whole must have benefited considerably, directly through hearing the opinion of leading ecologists from other lands on types of vege- tation underfoot or overhead, indirectly through the bond of comradeship thus instituted for the future. The organisation of such an excursion can only be appreciated by those who take some part in it, and most of the members did so. When success comes to such a scheme, it is generally due to the one or to the few who undertake the arrangement of the multitudinous detail involved. The existence of the Committee made it possible to spread the work over a fair number of individuals, but the real weight fell mainly on one, and at the most recent meeting the usually informal evening meal became a function with speeches which con- veyed to the leader of the I.P.E. the Committee's expression of appreciation of a good thing well done.

Ordinary Excursions.

Less ambitious excursions have been a prominent feature, especially of the spring meetings. In April, 1910, from London, an excursion was made from Oxted to Westerham on the borders of Kent and Surrey, mainly for the observation of the woodland types, beechwoods on the chalk escarpment being strongly contrasted with the oakwoods on " clay with flints." A few days before Christmas, 1910, excellent weather conditions were obtained for an examination of the sand-dune vegetation at Southport and so far as the winter phase and the distribution of associations were concerned, the

excursion was a profitable one. The geographical position of Aberystwyth (April, 1911) with its long railway journey naturally produced a small meeting, but those members present spent the greater part of three days in the field under the guidance of Professor Yapp. One day was given to Borth, an extensive tract of lowland bog, which on its seaward margin is now being invaded by estuarine mud, sand, and banks of shingle, each bearing its distinctive vegetation. Another day was spent in the extensive oakwoods between Aberystwyth and Devil's Bridge, which are of the *Q. sessiliflora* type and very uniform, but present a series of interesting variations in the neighbourhood of springs and flushes.

NOMENCLATURE.

The proposal to discuss phytogeographical nomenclature at the International Congress of Botanists at Brussels in 1910 gave the Committee an opportunity of formulating its views. On the invitation of the Reporters of the Commission of Phytogeographical Nomenclature (Professors Flahault and Schroeter), several members took part in an attempt to formulate the general view of the Committee. At the Cambridge meeting (April, 1909) certain theses were put forward for discussion with the result that a scheme was elaborated and submitted to the Reporters, and was later printed in the " Reports and Propositions on Phytogeographical Nomenclature" for submission to the Congress. The crux of this document was : "that the term plant-formation should be applied to the fundamental unit of vegetation" and "that the view put forward by Moss (Geographical Distribution of Vegetation in Somerset, 1907, p. 16) which regards the plant-formation as the series of natural phases of vegetation occurring in a given habitat, is strictly in line with its historical development, since it emphasises the habitat as defining the formation." This concept led to correspondence with the Reporters, who adopted the definition of E. Warming (Œcology of Plants, 1909), or, as they expressed it, "we can consider a formation as an actual expression of certain conditions of life independent of floristic composition." They also contended that Moss's view introduces hypotheses and subjectivity. The later publication " Fundamental Units of Vegetation" by Dr. Moss (1910) appeared about this time, and presented an historical inquiry into the use of "plant-formation" and other terms, and the view put forward there (p. 36) seemed to the Committee to express the general concept so well that they adopted it and submitted (January, 1910) a set of resolutions in support, which were published in the " Reports and Propositions" along with an appendix—" Criticism of the attempt to determine plant-formations by 'growth-forms' (Warming, 1909)," by A. G. Tansley and C. E. Moss.

Several members of the International Commission voted in favour of accepting the British Committee's view of the concept of the plant-formation, but at an informal meeting of phytogeographers which took place in Brussels during the sittings of the Congress, at which the British Committee was represented by Mr. A. G. Tansley, it became clear that no general agreement on this point could be hoped for, and the Reporters very wisely decided not to put forward

any propositions which would not command unanimity, and contented themselves with a few safe propositions (see " The Brussels Congress of Botanists," New Phyt., Vol. IX, 1910, p. 261).

A very minor detail of nomenclature should be recorded—that the Committee has sanctioned the use of " British Vegetation Committee " as an alternative short title, in place of the somewhat cumbrous, if comprehensive, " Central Committee for the Survey and Study of British Vegetation."

PUBLICATIONS.

" Types of British Vegetation " as the first essay of the Committee in book form is an important landmark in the Committee's history. The first proposal was a guide-book for the I.P.E., but it was soon evident that even the most meagre summary of existing publications would extend to many pages and consequently be expensive to produce. The Syndics of the Cambridge University Press were then approached, and agreed to publish a general work embodying our existing knowledge of British Vegetation, and it was felt that such a work, if the more general accounts were illustrated by the localities to·be visited by the I.P.E., would constitute the best kind of guide-book that could be desired. The further evolution of the book is indicated in the Editor's preface. What the Editor does not say is that the book involved a great deal of work, which had to be done under pressure in a very short time, and no record would be complete which did not emphasise the Committee's indebtedness to the Editor. The direct contributors include seven members of the Committee, but practically every member has directly or indirectly contributed to the book. It is a record of much that has been done, but one of its chief uses will be to indicate how much there is still to do.

The Committee has issued two pamphlets, reprints from this journal. " The Fundamental Units of Vegetation " by C. E. Moss (1910) was adopted as a pamphlet because it is a very useful historical record of the evolution of the development of the concepts of plant-formation and plant-association from early writers like Grisebach, through a long and varied subsequent career. The author endeavours to bring out the main line of development running through the various uses of these terms, and to show that its most natural culmination are the concepts already referred to.

" The Woodlands of England " (1910) was also adopted as a Committee pamphlet because it brought together and classified the observations of the authors on Woodlands over the greater part of England, and presented, for the first time, a logical scheme of their inter-relations.

There has also been published under the auspices of the Committee " The Vegetation of Caithness considered in relation to the Geology," (1910), by C. B. Crampton. This, it is hoped, may be a new departure, which will facilitate the publication of larger memoirs. The Committee has at present no fund for publications, but in the above case the Carnegie Research Fund defrayed the cost after the manuscript had been reported on by the Primary Survey Publications Sub-Committee of this Committee, which some years ago was established as a medium for consideration of

memoirs dealing with vegetation on broad " primary " lines. The Caithness memoir introduces into studies on vegetation, the importance of the topography of a district on the distribution of plants both now and in the past. It also includes as a major theme, the distinction of plant formations (*e.g.*, moorland) on relatively stable geological substrata, and the more transient associations on unstable substrata, such as those presented by the erosion and deposition by rivers and seas, or by the climatic factors so actively at work amongst arctic-alpine vegetation. Owing to the conditions of the grant this paper cannot be purchased, but it has been widely distributed, and applications to the the author (or to the Secretary of the Committee, 13, George Square, Edinburgh), will be considered.

Numerous other publications by members of the Committee have appeared in the various periodicals, but these need not be specifically recorded.

Altogether the British Vegetation Committee has passed through a somewhat eventful period, the prelude, it is hoped, to even greater and more widespread future activity.

W.G.S.

NOTES ON RECENT LITERATURE.

RUST FUNGI.

The Wintering of *Puccinia graminis*.

Pritchard[1] discusses the various possible means by which *Puccinia graminis* survives the winter and causes infection of the wheat fields of the northern part of the United States year after year. He considers that the aecidiospores play a relatively small part in the dissemination of the fungus, for he found that the direct influence of infected Barberry bushes was confined to a distance of 100 yards. Furthermore he experienced considerable difficulty in artificially infecting wheat plants with aecidiospores. It is well-known that the Barberry is by no means always necessary for the propagation of the black rust of cereals, because no infected Barberry bushes have ever been found in Australia and Ecuador where this rust is prevalent. According to Pritchard the uredo-spores do not retain their vitality over the winter in the State of North Dakota, so that this source of re-infection is excluded. Uredo pustules appear on winter wheat there as early in the year as upon wild grasses, and therefore the latter can hardly be looked upon as the source of infection of the wheat plants.

[1] Pritchard, F. J. Bot. Gaz., 1911, Vol. 52, p. 169.

Pritchard inclines rather to the view that infection is carried from year to year mainly by means of infected seed. He points out that teleutospore pustules of *Puccinia graminis* are of frequent occurrence on wheat grains, and he brings forward evidence that fragments of living mycelium are to be found in such grains in the cells of the scutellum close to the growing point. It is obviously difficult to determine what this mycelium is, but the possibility of it belonging to *Puccinia graminis* must be considered. Pritchard supposes that this mycelium invades the embryo at the time of germination and thereby causes the infection of the young plant.

In a second paper the same author[1] gives the results of a further investigation of the same problem. Rusted wheat grains and their seedlings were microtomed and examined for the purpose of tracing the mycelium previously mentioned. Pritchard has no doubt that the mycelium found in the young roots and stems of such seedlings belongs to *Puccinia graminis* and that it has been derived from the mycelium associated with the spore pustules in the pericarp of the grains. This mycelium passes upwards mainly in the spaces between the leaf sheaths, though branches pass also into the tissues. The nuclei of the hyphæ are generally associated in pairs, a feature agreeing with the nuclear characters of the mycelium of *Puccinia graminis*.

The author made no attempt to follow this mycelium onwards until the time of spore formation. This would have been a laborious undertaking, but the results obtained from it would have been of great interest and would have made, perhaps, the evidence even stronger than that now brought forward. All the plants used in the experiments were fixed for microscopic investigation when they were about 10 inches high, and so none were left for the investigator to see at what date, if at all, uredo pustules developed upon them.

The proposition brought forward by Pritchard is more tangible than Eriksson's well-known mycoplasm hypothesis, and it is certainly the best evidence we have yet that the earliest outbreaks of black rust in the year are due to contaminated seed.

The Biology of the Uredinales.

An interesting commentary on recent work in this group of fungi appears from the pen of R. Maire.[2] The cytology and systematic position of the group are first discussed. In regard to the origin of the Uredinales, Maire considers that they have come from the same stock as the rest of the Basidiomycetes, and thinks that this common origin is to be sought amongst the ancestors of the Ascomycetes.

In his classification of the group from the standpoint of general life-history, Maire ceases to use the term " Lepto " as applied to certain forms. The Uredines, whose only functional spore form is the teleutospore, were formerly divided into two groups, the Lepto-forms whose spores germinated immediately after formation, and the Micro-forms whose spores germinated only after a period of

[1] Pritchard, F. J. Phytopathology, 1911, Vol. 1, p. 150.

[2] Maire, R. Prog. Rei Bot. 1911 Vol. 4, p. 109.

rest. Maire points out that in *Puccinia malvacearum*, formerly described as a Lepto-form, the germination of the spores is immediate or retarded according to external conditions, and hence concludes that there is no essential distinction between the Lepto and the Micro-forms.

Maire discusses many of the interesting features presented by the general biology of these fungi. His verdict upon Eriksson's mycoplasm hypothesis is an open one, but the arguments advanced against it by Marshall Ward have lost none of their force with the lapse of time.

Maire enters upon a consideration of the possible ways in which so many Rust Fungi have developed a heterœcious habit. According to Fischer's views, a rust, at present heterœcious, may have formerly been pleophagous, and in the process of evolution may have come to develop its æcidial stage only upon certain of its former hosts and its teleutospore stage upon others. Dietel, however, holds the view that the ancestral forms of the heterœcious rusts possessed only teleutospore stages and that other spore forms were subsequently elaborated ; the teleutospore stage then lost the power of completing its development on the original host and by some means or other passed to a different host. In a recent book Olive[1] supports the same view. He considers it likely that the present gametophytic host is relatively the primitive one, and that heterœcism has been evolved by the passing of the sporophyte generation to a new host. Olive mentions the fact that the sporophytie generation of many rusts has a tendency to a pleophagous habit. Thus *Melampsorella caryophyllaccarum* attacks only *Abies* in its gametophytic phase, while its sporophyte is found on no less than five different genera. Nevertheless the gametophyte is sometimes plurivorous, and Maire mentions the extraordinary case of *Puccinia Isiaceæ*, whose teleutospore stage is formed only upon *Phragmites communis*, but whose æcidia are produced upon no less than twenty-two hosts, belonging to nine different families. It is interesting to note that in the only known heterœcious Asco—mycete, viz., *Sclerotinia Ledi*, there would appear to be no relation between the alternation of hosts and the gametophytic and sporophytic stages of the parasite. As yet we know very little of the physiology of heterœcism, and until more knowledge is forthcoming it is difficult to see how we can obtain any clear indication of the manner in which a heterœcious mode of life has been evolved.

F.T.B.

[1] Olive, E. W. Phytopathology, 1911, Vol. 1, p. 139.

THE CLASSIFICATION OF LICHENS.

Since the publication in 1894 of the first part of this Monograph[1] many advances have been made in the study of lichenology, and consequently the classification used by Crombie has been

[1] "A Monograph of British Lichens," Part I, by the Rev. J. M. Crombie, M.A., F.L.S., 1894. Part II, by Annie Lorrain Smith, F.L.S., 1911. Published by the British Museum.

considerably modified, though, owing to the necessity of keeping up some show of uniformity, the modifications have probably been fewer than they otherwise would have been.

The students of lichens during the last twenty years have not been numerous, but the work of Zahlbrucher, Boistel, Jatta, Schneider, Bruce Fink, Hue, Miss Smith and others has placed lichenology on a different footing, and rendered some changes in classification and nomenclature absolutely necessary. When Nylander, Fries, Lindsay, Leighton, Mudd and Crombie described, figured, named and classified lichens, the real nature of these curious plants was unknown or a question of great controversy, but to-day few workers doubt that the structure of these plants is due to mutualism.

In classifying them some difficulty is experienced in deciding on what symbiont the system should be based, whether the fungal or the algal constituent should be the determining factor to the systematist.

In all groups of plants the organs of reproduction are held to be of higher systematic value than the vegetative portions, and as the spore-bearing organs (asci) are those of the fungal symbiont the main lines of classification are generally determined by the fungal component of the plant.

The old methods of classification into gelatinous, fruticose, foliaceous, and crustaceous lichens[1] has had to be practically rejected.

A system of classification should take into account not only the present structure of the plants involved, but also their evolutionary history, interpreting the former in terms of the latter. This is a complicated business in a composite group such as the lichens, for even if the ancestors of the symbionts have not been eliminated, the modifications induced by their mutualism may have been so great that it is now almost impossible to trace them.

The Basidiolichenes, in which the fungal ancestors belong to the Basidiomycetes, are not represented in this country, all the species included in this monograph belonging to the Ascolichenes, with apothecia or perithecia similar to those found in the Ascomycetes.

The system adopted by Crombie in the first part of this monograph is apparently not followed by Miss Smith, judging by the modifications introduced into the second part, and the arrangement of specimens in the lichen cabinet of the Natural History Museum.

Ephebacei and Collemacei of Crombie's system, as well as all the other lichens (Stictinei, Peltigerei and Pannariei) having a more or less gelatinous thallus and blue-green algal cells are placed under Cyanophila, the algal constituent having the preferential treatment as a systematic base. Pyrenidium, because of its perithecial method of reproduction, is now transferred to Pyrenocarpei.

The modern group of Coniocarpi or Coniocarpineæ corresponds to Crombie's series Epiconoidei, in which, at maturity, the spores form a powdery mass on the surface of the apothecium.

Parmeliales include most of the genera placed in Crombie's

[1] See Vines' "Student's Text Book of Botany," 1896.

Ramolodei, Phyllodei and Placodei, having lecanoroid or parmelioid apothecia, the margins or rims being derived from the thallus.

Lecideales include Crombie's Cladodei, Gyrophorei and Lecideei, the apothecia being without thalline margins or algal cells. The family Cœnogoniaceæ is placed here, though the two British representatives, *Cænogonium ebeneum* and *Racodium rupestre* are invariably sterile.

The Graphidei (Graphidiales or Graphidineæ) correspond to the same groups in Crombie's synopsis, together with Dirina, Rocella and Lecanatis (five species of which were formerly included in Lecidea), the lirelline, rotundate, or irregular apothecia due to the probable Pharcidioid or Hysterioid ancestors of the fungal symbiont, being the determining features. Agyrium is now relegated to the Fungi, Rehm considering it to be a member of the Bulgariaceæ.[1]

The Pyrenodei (Pyrenocarpineæ) include Crombie's series of Pyrenodei and Peridiodei with the exception of the genera Strigula and Endococcus which are now classed as fungi. The determining factor in this group is the Pyrenomycetioid ancestor of the fungal symbiont, the sporocarp being a perithecium usually opening by an apical ostiole.

Myriangium, placed by Crombie in a distinct group, is now considered to be a fungus. In the monograph, Part II, the nature of the algal constituent is given, and, in some cases, the probable ancestry of the fungal constituent is referred to; but where the latter is indefinite, the somewhat speculative views of Schneider[2] have been generally, and, perhaps wisely, neglected, since the book does not pretend to be a text-book of lichenology, but an enumeration and description of British species.

The different series are divided into orders, and these again into many genera, useful keys being provided in each case, so that it is a matter of little difficulty for a lichen-worker to run down a plant to its proper genus.

The genus Lecidea is divided according to the form of the apothecium, number of spores in the ascus, and the colour and septation of the spores, into eleven genera, Gyalecta, Biatorella, Biatorina, Bilimbia, Bacidia, Buellia, Leciographa, Rhizocarpon, Bombyliospora, Lopadium and Lecidea, the last generic name being retained for some 200 species, having eight simple spores in the ascus.

In the Graphidiales, there are six British sub-divisions or orders, three of which, Dirinaceæ, Roccellaceæ, and Lecanactaceæ, were not placed by Crombie in his Graphidei.

Lecanactaceæ contains the genera Lecanactis and Platygrapha, the former genus consisting of five species separated from Lecidea, on account of the algal symbionts (Trentepohlia) and the form of the apothecia. Arthoniaceæ contains two genera, Arthonia and Arthothelium, the latter including two species with uniform spores, formerly placed under Arthonia by Leighton and Crombie. Chiodectonaceæ contains the genera Chiodecton, Glyphis, Enterographa and Sclerophyton, the last two being formerly placed in the genus

[1] Massee's "Fungus-Flora," 1895.

[2] "A Text-Book of General Lichenology," 1897.

Stigmatidium. Graphidiaceæ includes all the other Graphidei of Crombie, except the fungus Agyrium, as well as the genera Ptycho-grapha (with compound hymenium), Encephalographa (Lithographa with 1-septate, brown spores) Phæographis (Graphis with brown spores), and Graphina (Graphis with muriform spores).

The series Pyrenocarpineæ (Pyrenodei) is divided into seven orders and contains twenty-seven genera, only ten of which are given in Crombie's synopsis, the old genus Verrucaria now being split up into thirteen genera, according to the nature of the peri-thecia, paraphyses, asei, spores, and algal cells.

As noticed above many plants formerly classed as lichens have been placed as fungi parasitic on lichen thalli, and it is probable that some other so-called lichens will have to share the same fate ; *Arthonia punctella*, Nyl, while the book was in progress, has been classified as a discomycetous fungus and a note to that effect is given on p. 345. Agyrium, Strigula, Myriangium, Endo-coceus, and some species of Verrucaria have been rejected, while the positions of many other parasitic species are doubtful. *Dacampia Hookeri* (=*Lecidia Hookeri*), *Buellia parmeliarium* (= *Abrothallus* p.), *Arthonia varians* (= *Celidium* v.), *Biatorina epi-blastematica* (= *Scutula Wallrothii*), and other parasitic species included in the present work, have been and are still regarded by some authors as fungi.

A number of species for which Miss Smith is in no way res-ponsible, as she has had no opportunity of seeing them, have been included. Most of these unseens are Stirton's discoveries, and it seems a pity that they should not have been submitted to such a competent lichenologist as the authoress of this monograph.

Very few new records or new species have been added to the list, and it is pleasing to note that Miss Smith is somewhat conser-vative in this respect, since the lichenologist is already sufficiently puzzled by the minute differences between some so-called species.

The addenda contain most of these species or varieties new to Britain :—*Calicium roscidum, Cladonia luteoalba, Cladina implexa, Lecanora mongeotioides, L. Lillici, Lecidea pleiospora, L. declin-ascens, Biatorella campestris, Gyrophora spodochroa,* "*Inoderma byssacea,*" *Arthonia Lillici, Verrucaria prominula,* var. *minor, Gongylia viridis, Microglœna Larbalestierii, M. Holliana, Artho-pyrenia areniseda, A. foveolata, A. halodytes* var. *Hollii, A. Crombei, Leptorhaphis Carrollii, Microthelia dispora* and *Porina Curnowii.*

Botrydina vulgaris, which was placed by E. Acton in the lichens, is considered to be of doubtful position.

The plates are beautifully drawn and form a valuable adjunct to the descriptions, and the whole work is an essential and reliable book to any student who wishes to unravel the mysteries of this wonderful group of plants. W. WATSON.

ON SOME METHODS IN PALÆOBOTANY.

BY H. HAMSHAW THOMAS.

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THE remains of the plants of past ages have generally been pre-
served in two ways. The first is by petrifaction, when the
original cell outlines are preserved by the infiltration and solidifi-
cation of lime, silica or some similar substance. The second method
is by the formation of an impression or cast in a sandy or muddy
matrix, the original plant-tissue being reduced to a coaly layer.
But we have also in some cases a rather different form of preservation
from the last mentioned; here the plant has been embedded in mud,
little decay has taken place, and the remains which are now found
are best described as "mummified plants." In the case of leaves, the
cuticles of both surfaces often remain, sometimes with portions of
the tougher cells, the cellulose has become more or less converted
into carbon, and we have here a stage in the production of the
ordinary type of impression in which all the plant-tissue is reduced
to a thin coaly layer.

From the point of view of the botanist, of course, the petrified
plants are by far the most important. It has, however, rarely
happened that the conditions were suitable for the petrifaction of
plants, and even when we have petrified remains they are often very
fragmentary. Impressions are far commoner, and though we do
not gain so much useful knowledge from them, they often exhibit
the external features of plants with great clearness; they aid us in
piecing together scattered fragments of the various organs of a plant,
and sometimes furnish useful information as to the form of the
reproductive organs.

The mistakes of some of the earlier–and ever of the later–palæo-
botanists, whose observations were confined to plant impressions,

have inspired in the minds of many, a profound distrust for much of the work based on the study of impressions. But where the latter can be correlated with petrifactions or some knowledge gained of their structure, a comprehensive study of their external form may be of the greatest importance. In the case of mummified plants or of impressions in which the plant substance is not entirely destroyed, much information can usually be gained as to the form of the stomata, epidermal cells, spores, seeds, etc., by the use of suitable methods. This is especially the case with those Mesozoic plants which are preserved in fine shales or mudstones ; the tissue has not yet become completely carbonised, and the remains of the plant can usually be easily detached from the matrix. These plants are especially worth study because we know of so few localities in which petrifactions of this age are found, and hence we have comparatively little knowledge of the affinities of many Jurassic plants, at the same time they are the key to many of the most discussed phylogenetic problems. In these circumstances a close study of the remains which have hitherto been regarded as structureless may lead to interesting results.

The object of these notes is to give a brief account of some of the methods which have proved useful in studying Jurassic plants, chiefly of the mummified or impression type.

PREPARATIONS OF LEAF CUTICLES.

These can be readily made from specimens of plants which originally possessed a fairly thick cuticle and which are preserved in a fine grained matrix from which they can be easily detached. It was shown by Borneman in 1856 that the carbonaceous material could be dissolved out by using Schultz's solution, and the method has since been used with considerable success by Schenk, Zeiller, Nathorst and others.

The following method may be employed. A portion of the leaf is chosen in which the tissue shows a tendency to peel off, and some of it is removed with a needle. If a drop of water is previously placed on the spot, it often renders the removal of the tissue easier. The detached fragment is then placed in a shallow china pan of the type used by artists for mixing water-colours (these pans are circular and are made in sets, one fitting on top of another and acting as a cover), a little powdered Potassium Chlorate is sprinkled on it and a few drops of moderately strong Nitric Acid added. The pan is covered up, labelled, and left to stand for some time. Watch-

glasses may be used instead of the china pans, but are not so stable and it is by no means pleasant to spill the strong acid solution. After a time, varying with different specimens from three or four hours to as many days, and depending on the strength of the acid and on the material of the leaf, the specimens become clear brown in colour. The acid is then decanted off, the specimen is washed with water and freed from any surface particles by the use of a fine brush. A few drops of ammonia solution are then added, which cause the cuticle to become black at first, but which later brings about the clearing of the specimen and the solution of the dark substances. If the process has been complete a more or less clear membrane is left, but care must be taken to separate the cuticles of the upper and lower surfaces at this stage, otherwise a clear view of neither will be obtained. This separation is usually a matter of some difficulty, but may be assisted with needles and by using the sharpened point of a match. If the specimen does not become clear it may be washed and replaced in fresh acid and the process repeated. Some leaves may require treating for a considerable time before becoming transparent. The resulting cuticles are washed with water and may be stained or mounted directly. I often employ as a mountant pure Glycerine in which Zinc Sulpho-Carbolate has been dissolved (the latter substance improves the optical properties of the glycerine). The slides may be conveniently sealed with wax,[1] but if they are to be kept for a long time a coating of gold size should be added to prevent the wax from cracking.

Preparations made in this way often yield a surprising amount of information about the form of the epidermal cells, the shape and distribution of the stomata. If hairs or papillæ were present, they are clearly seen, while portions of the more resistent sub-epidermal tissue, fibres, etc., may occasionally be found. It seems probable that the study of the stomata may be useful not only in classifying the fronds from which they are obtained, but also in investigating their relationships and phylogeny.

The Study of Sporangia and Spores.

Careful search in fine grained fossiliferous shales often results in the discovery of fertile specimens of ferns, conifers, etc. The sporangia of ferns are often quite clearly preserved though converted into carbonaceous material, and the annulus, if present, can be clearly seen. The prismatic binocular microscopes made by

[1] See NEW PHYT., Vol. X, p. 105, 1911.

Zeiss are of the greatest service in the examination of these and similar opaque objects. Even if the sporangia cannot be clearly made out, preparations of the spores can be readily obtained. The cutinised exospore wall seems to be almost indestructible and if embedded in a suitable matrix remains unaltered for an indefinite period and can be obtained by dissolving away the surrounding material. Thus spores can be obtained from Carboniferous and Jurassic plants by treating them with Nitric Acid and Potassium Chlorate in a similar way to that used for the leaf-cuticles. If the sporangia are small it is best to remove them from the rock with a needle and place the fragments on a glass slide possessing a small concavity. A drop of Nitric Acid and a few tiny crystals of $KClO_3$ are placed on the fragments and the slide is put under a small bell-jar with a dish of water, or between two watch glasses the lower of which contains some water. In this way it may be kept for a day or two without the acid drying up. When the carbonaceous fragments have turned brown they are carefully washed with water and a drop of dilute ammonia is added. This at once dissolves away the opaque material and the spores are liberated. The spore-walls show the markings they originally possessed, and the tetrahedral or lateral scar indicating their mode of origin is usually seen. The preparation and permanent mounting of spores in this way requires very cautious manipulation, but by using a glass slide on which the whole process is carried out, the progress of the reaction can be watched under the microscope. The fact that microspores are preserved in this way is most useful, especially when we are dealing with structures which appear to be like sporangia, for we can easily test whether they are really of this nature, and whether they are micro- or macrosporangia. It appears as though the megaspore membrane were cutinised in the same way, and if we apply the same method of treatment to seeds it is remarkable how many tissues become visible and seem to have escaped destruction. In some such seeds the outside of the integuments, the megaspore membrane and remains of fibrous cells been visible ; traces of thickened hypodermal cells and portions of tracheids may also be seen occasionally.

Cedar-Wood Oil.

The examination of indistinct or badly preserved opaque objects under the binocular microscope is often facilitated by the use of cedar-wood oil and strong illumination. A drop or two of oil placed

upon the object has the effect of differentiating its parts more clearly, of bringing out any slight differences of colour and of making minute veins or markings more easily visible. As is well known, water has a somewhat similar effect, but it quickly soaks in and often destroys the specimen, on the other hand the oil dries up slowly after use without damaging the specimen at all. This method was devised by Dr. T. G. Halle of Stockholm.

The use of oil in the same way has proved very helpful in examining the polished faces of blocks of petrified material especially where the cell walls had lost their colour and were almost invisible without such treatment.

THE COLLODION METHOD.

In cases where the cast of the epidermal cells of a leaf have been retained in fine grained material such as tufa, the microscopical features of the original cells can often be made out by taking a collodion cast of the fossil. Accounts of this method have been published by Professor Nathorst[1] and Dr. Bather[2]. The process is very simple, a drop of collodion is placed on the surface of the fossil and allowed to dry; as it dries, it peels off the rock, and if subsequently mounted and examined under the microscope it may show clearly the outlines of the epidermal cells. I found great difficulty at first in employing this method successfully. The collodion dried slowly to a whitish semi-opaque film which often adhered firmly to the specimen and could only be removed with difficulty. This seems to be due to the composition of the collodion, and the ordinary British Pharmacopœia solution is quite unsuitable. It apparently contains too much alcohol to allow the rapid drying of the film, but by allowing a quantity of this original solution to evaporate to a jelly and redissolving it in ether, a solution was obtained which dried rapidly, peeled off the rock readily and gave a transparent film.

I have not found this method very useful when working with Palæozoic and Mesozoic impressions because it is seldom that the matrix was suitable for retaining a cast of the epidermal cells. It is, however, of considerable value in dealing with petrified wood, etc. Films taken from freshly fractured surfaces, often show as much or more than a thin section cut in the same direction through the specimen. It is therefore of great use in a preliminary study of material and for comparison with sections. In order to get perfectly

[1] Ark. för Botanik VII, p. 1, 1908.
[2] Geol. Magazine, Decade V, Vol. V, p. 454, 1908.

clean films from a surface, several preliminary casts should be taken and discarded, all the loose material will be picked off with the earlier films, and the surface left quite clean.

It seems probable that a renewed examination of fossil plants by some of the methods just described will result in great additions to our knowledge of their structure and affinities. The elaboration of these and similar methods is giving a new impetus to the study of what has been hitherto regarded as very unpromising material from a botanical standpoint. Most of the methods described in these notes were devised or improved by Professor Nathorst of Stockholm, who has done so much for the study of Jurassic plants and to whom the thanks of the author is due.

THE INTERNATIONAL PHYTOGEOGRAPHICAL EXCURSION IN THE BRITISH ISLES.

VI—Some Remarks on the Floristic Results of the Excursion.

By C. H. Ostenfeld.

Owing to the excellent manner in which Mr. Tansley had arranged the conditions for preparing herbarium plants during our excursion, it was possible, in spite of the short time, to make ample collections at all points of our extensive trip. To me it was of special interest to get as many British plants as possible, as I was anxious to compare them with more northern and with Danish plants. I devoted special attention to the forms of the more critical species, and have brought home a large number of such plants. My leading idea in so doing is that a study of the geographical distribution of the " elementary " species or forms may be of value with regard to the interpretation of the immigration of the postglacial flora and the paths which this may have followed. As illustrations of my point of view the two races of *Helianthemum nummularium*, viz., var. *hirsutum* and var. *tomentosum* may be cited. In Denmark we have the former almost alone, while in the British Isles only the latter is found ; this means that one variety has travelled in a western direction, the other in a northern, since both occur in Central Europe, Very much the same is the case with the two varieties of *Lamium galeobdolon*, of which var.

montanum is British, var. *vulgare* is more eastern and northern (Denmark and South Scandinavia). In other instances the British Isles have the same variety or species as Scandinavia, e.g., *Alchimilla acutidens* and *Erigeron borealis.* Such is the case with regard to the more northern forms, which must have come to the British Isles soon after the Ice-age and which are now confined to their northern and " alpine " regions, while they also occur in the Scandinavian mountains. In yet other instances the British Isles harbour more than one race, e.g., *Scirpus cæspitosus* var. *austriacus* and var. *germanicus*, and *Rumex acetosella* var. *acetoselloides* and var. *angiocarpus*, which have different geographical distributions elsewhere.

These examples may bring out what I mean, and I think comparisons on these lines must give us a better understanding of the paths of postglacial immigration and of various problems of floristic phytogeography relating to those countries which are supposed to have been wholly covered by the land-ice and are consequently inhabited by a flora of postglacial origin.

In the following pages I am publishing some results of the examination of my collections, and I hope they may be of interest to British floristic phytogeographers. I know they are very incomplete in many respects, and if they stimulate further studies in this direction, they will have done their duty. Undoubtedly much that is here written will have to be corrected or abandoned.

I have only dealt with some scattered genera, as my friend, Mr. G. C. Druce, has already published a full report on the floristic resuts,[1] and he is, of course, much more competent to tell what is of interest in the British flora, than I a foreigner. But, at least, these notes may serve as a further proof that the brilliant excursion has had results in the floristic direction.

The sequence in the natural orders is that adopted in the British floras, *e.g.*, Babington's " Manual."

RANUNCULACEÆ.

Ranunculus, Sect. *Batrachium* S. F. Gray. In Denmark and Scandinavia the authors mostly follow the excellent monograph of the species of water-crowfoot, published by my late friend O. Gelert (Botanisk Tidsskrift, vol. 19, 1894, Danish with French résumé), according to whom the number of species is rather restricted and each species is very variable. Using this monograph as a standard, I have noticed from our excursion (besides *R. hederaceus* L), two species, viz., *R. paucistamineus* Tausch var. *Drouetii*

[1] NEW PHYT., Vol. X, pp. 306—328 1911.

(F. Schultz), Marss. from the river at Monsal Dale, Derbyshire, and *R. peltatus* Schrank, f. *truncata* Koch from a small rivulet at the Upper Lake, Killarney.

NYMPHÆACEÆ.

Nymphæa (vel *Castalia*) *alba* L., var. *occidentalis* Ostf., nov. var.

Differt a specie : Nervis loborum folii primariis si in lineam rectam producas, convergentibus; receptaculo ad insertionem subangulato ; fructus parte summo cicatricibus staminum destituta ; seminibus majoribus (3—3·5 mm.)

Differt a subspecie N. *candida* Presl. : Granis pollinis verrucoso-papillosis; carpellorum numero majori ; radiis disci stigmatici unicuspidatis flavis ; germine sub disco minus angustato ; fructu globoso vel depresso-globoso (5 : 7).

Hab. Scotia (Perthshire: Loch Cally prope Dunkeld) et Hibernia (Galway: Craigga More).

The small waterlily found during the excursion, first in Scotland and later in Ireland, was provisionally identified by me as *Nymphæa candida* Presl., and this determination has been followed by Druce in his paper on the " Foristical Results " (l.c. p. 324, New Phytologist), where he quotes the description of *N. candida* Presl. from H. S. Coward, The Waterlilies, (Carnegie Publ., 1905). This description, compiled from different sources, and also the better descriptions in Caspary's different papers, do not wholly
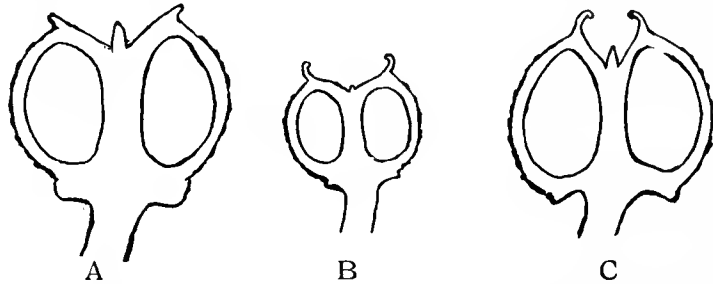
Nearly ripe fruits in longitudinal section. Two-thirds nat. size.

A. *Nymphæa alba* (from Denmark), alcoholic material. B. *N. alba* var. *occidentalis* (from Craigga More, Co. Galway), soaked herbarium material. C. *N. candida* (cultivated in the Botanical Garden, Copenhagen), alcohol material.

agree with our Scottish and Irish specimens. I was, therefore, in some doubt as to the correctness of my identification, and have now examined my specimens more closely and have compared them with numerous specimens of *N. alba* and *N. candida* from Sweden and Eastern Prussia, Bohemia, etc. The result is that *the British plant is not the true N. candida*, to which it has a strong external resemblance. The above given diagnosis will show that it is intermediate between the two forms; having some characters of *N. alba*, others of *N. candida.* Ascherson and Graebner (Fl. Nordostdeutsch. Flachland, 1898–99, pp. 319, 320) also mention, that while the two forms are well distinguished in Prussia, they have often met with forms in Pomerania and Brandenburg : " die sich mehr u. mehr der *N. candida* nähern, ohne ihr jedoch gleich zu kommen, so dass hier eine scharfe Grenze nicht vorhanden ist. Wir haben es hier augenscheinlich mit einer in der Ausbildung begriffenen Art zu thun." I think something like this is the case

with regard to the British form, but I should prefer the expla-
nation that we have, on the Continent, two forms, *N. alba* and
N. candida, and besides these, in the western part of Europe, our
plant, which may also occur in Norway (in our Copenhagen
herbarium I have seen a poor specimen which may be referred to
it). This form seems to inhabit pools and small lakes in moors,
while the true *N. alba* (as we saw it in the Norfolk Broads),
prefers less "acid-humus" water. The true *N. candida* is a
northern and eastern form; R. Caspary, "Botan. Notiser," 1879,
says " per Europam et Asiam borealem et arcticum et in regione
montana Germaniæ, Austriæ et Asiæ (Himalaya); our form is the
western substitute; the main species *N. alba* occurs in the whole
of Europe and Siberia (excluding the Arctic part), and also in
Algeria.

I recommend the form here described to closer examination
and comparison with the other forms, preferably under cultivation.

It is smaller in all directions than the ordinary *N. alba*;
Leaves 9–12 cm. broad, 11–13 long ; diameter of the flower 8–9 cm.

CISTACEÆ.

Helianthemum nummularium (L.) Dunal (= *H. chamæ-
cistus* Mill), v. *tomentosum* (S. F. Gray).

W. Grosser (Cistaceæ, in Das Pflanzenreich, 1903), has
divided this species into two sub-species, and C. K. Schneider
(Handb. d. Laubholzkunde, 8. Lief., 1909) follows him in this
regard ; while E. Janchen (Die Cistaceen Österreich-Ungarns, in
Mitteil d. Naturv. Vereins an der Universität Wien, 1909) has
several separate species under the *species collectiva H. chamæcistus*
Mill.

Whether we follow the first or the latest author, we find
two " forms " occurring in the more northern (not alpine) parts of
the area of the *species collectiva*. The question then arises which
form occurs in the British Isles, or do both forms occur ?
As far as I have seen, only the var. *tomentosum* (S. F. Gray) is
British (while in Denmark we have almost only the other form :
var. *hirsutum*, Thuill.), but I have had very few specimens from
Great Britain at my disposal, and further examination of more
ample material may result in discovering the other form also.
The var. *tomentosum* is easily distinguished by the felty, whitish
underside of the leaves; var. *hirsutum* has the underside of the
leaves green and covered with sparse steleate hairs.

As the two forms do not differ from each other in other more
important respects, I find it more natural to follow Grosser and
Schneider in taking them as two varieties of one species, than to
consider them as two species as Janchen does.

CARYOPHYLLACEÆ.

Sagina procumbens L. ✕ *saginoides* (L.) Dalla Torre. = *S. media*
Brügg (Syn. *S. glabra* Druce, 1911, non Fenzl, 1833.

On Ben Lawers we met in plenty a *Sagina* with white petals
about as long as the sepals. As there were many specimens and the
numerous flowers were open in the sunshine of the forenoon, the
plant attracted much attention, and caused much controversy

among the members of the excursion. I suggested that it was a hybrid between *S. procumbens* and *S. saginoides*, both of which were found, but, the latter, at least, only in the fruiting stage. Now when examining more closely the specimens brought home I must insist that my suggestion was quite right, as far as it is possible to identify the hybridity of a plant which is found growing wild and has not been produced by an artificial crossing.

My friend Mr. Druce (l.c. New Phyt., Vol. X, pp. 316 and 325) held that the plant in question must be taken as a variety (var. *scotica* Druce of *S. glabra* Fenzl., a mountain species from the Alps, the Italian mountains, Corsica, Sardinia, etc. I think, on the other hand, that it is not permissable to refer the Ben Lawers plant to *S. glabra* ; the latter has petals one-and-a-half times to twice as long as the sepals (our plant had petals not, or scarcely, exceeding the sepals), while the sepals and often the uppermost parts of the flower-stalks are glandular-hairy (glabrous in our plant) ; further the South-European plant is more woody and has larger flower-dimensions ; and lastly it is quite fertile.

The Ben Lawers plant is practically sterile ; when examining numerous specimens I found a few capsules containing seeds, but only very few of the seeds were fully developed, the remainder being small and hardly capable of germination. Mr. Druce's statement that the capsule is " somewhat smaller " shows that in his specimens also the capsules were only partly fertile. The plant stands in all its characters between the two putative parents ; it has mostly pentamerous flowers and the petals are as large as those of *S. saginoides*. It has the growth of *S. procumbens*, and this character is of importance, as no doubt the cause of its abundance on Ben Lawers. Small branches of barren shoots are easily broken off from the stem and carried away by the flowing water, and thus the plant is most common along water-courses. It behaves just as hybrids so often do : it is nearly sterile, but propagates profusely by vegetative shoots, and it is more vigorous and the specimens larger than is the case with the parents; further sterile hybrids very often flower much longer than the parents, because they continue to produce new flowers at a time when the parents are fully occupied in ripening their fruits.

The arguments brought forward by Druce are thus shown to be no arguments against the supposition of hybridity.

It is probable that this hybrid will be found to be rather common in places where both the assumed parents grow together, just as I have found that the hybrid *S. procumbens* ✕ *subulata* is is rather common on the Færöes, and behaves in the same manner as the Ben Lawers' hybrid does, having large and vigorous specimens, propagation by detached vegetative shoots, and sterility. This last hybrid is distinguishable from the Ben Lawers' glandular plant by the hairs on the sepals and uppermost part of the flower-stalk.

According to my view *S. glabra* Fenzl. must then disappear from the British Flora as suddenly as it has appeared.

GERANIACEÆ.

Geranium Robertianum L. var.

As far as I am able to understand the segregates of *G. Roberti-*

anum which A. Jordan has described (*G. modestrum, G. villarsianum*, etc.), the specimens collected in West Ireland on our excursion do not belong to them. Rouy and Foucaud (Fl. de France, vol. 4, 1897, p. 95), admit under *G. Robertianum* (besides some forms of lower rank) only one "forme" (*i.e.*, sub-species), viz., *G. purpureum* Vill., and under this sub-species they have arranged a whole series of Jordan's segregates. I think this arrangement is very good. The true *G. Robertianum* L. has more or less hairy carpels which have rather few and distantly placed transverse ridges (often branching), mostly larger petals and red anthers; its leaves are several times pinnatifid. *G. purpureum* has glabrous carpels with many and densely placed transverse ridges (not branching), smaller petals and yellow anthers; its leaves are not so many times pinnatifid.

According to the description a plant found in Cornwall (see Bot. Exchange Club Rep. for 1910), must belong to *G. purpureum*, but our Irish plants (from Clifden, Co. Galway, and Ballyvaghan, Co. Clare) do not; they have carpels of the true *G. Robertianum*, and must be referred to it. They have not the external habit of the typical *G. Robertianum*, and the flowers are considerably smaller, etc.; it is therefore probable that they represent a special variety, which has to be examined under cultivation and perhaps should have a name, but they must not be identified with *G. Villarsianum* Jord. or *G. purpureum* Vill.

ROSACEÆ.

Alchimilla acutidens, Buser, Lindb. fil. ampl.

The record of this "species" of *Alch. vulgaris* on Ben Lawers (alt. 400 to 800–1000 m.) is rather interesting from a phytogeographical point of view. It is an alpine and northern species which according to H. Lindberg's monograph (Die nordischen Alchemilla vulgaris -Formen und ihre Verbreitung, Helsingfors, 1909), is found in Russia, Finland, Sweden (southward to ca. 59^0 N. Lat.), Norway, the Faröes and Iceland, besides the Alps. It was rather surprising that it was not known from the Scottish mountains before, although Dr. Lindberg had abundant material of *Alchimilla* from the British Isles for examination. Now, that we have found it on Ben Lawers,—and no doubt it will be found elsewhere in the Scottish Highlands,— a gap in its area of distribution has been filled up.

The "species" is very near the common *A. alpestris* Schmidt, from which it differs in the following points :—

The flowering stems sparsely covered with adpressed hairs in the lower part up to the second (or third) branch; the leaf-stalks also bear adpressed hairs, as do the nerves of the leaves on the underside and generally the outermost part of the basal lobes; leaves orbicular or reniform with 9(-11) lobes; teeth uniform, acute; apical tooth as long as and uniform with the others. Apart from the distribution of hairs here described the plant is glabrous (with the exception of the hairs on the tips of the leaf-teeth). *A. alpestris* bears still fewer hairs; only the leaf-nerves of the underside are hairy on their distal halves, and the stems and leaf-stalks are very slightly hairy; the teeth of the leaves are not so uniform nor acute, and apical tooth is smaller than the others.

Sorbus aucuparia L. var. *flava* Druce, New Phyt., 1911, p. 312.
The form with orange-yellow ("*aurantiacus*") fruits seems not
to have been described before, as it is different from *S. aucuparia*
var. *Fifeana* hort. (cf. Ascherson and Graebner, Snyopsis VI, 2,
1906, p. 88), which is a yellow-fruited form of the hairy variety
(var. *lanuginosa* (Kit.) of the mountain ash. The Irish yellow-
fruited form belongs to the var. *typica* of the species. I only
saw one tree at Roundstone (Galway), and two trees, far distant
from each other, in the wood at the Upper Lake, Killarney.

DIPSACACEÆ.

Succissa præmorsa (Gil.) Aschers., var. *hispidula* Petermann, Fl.
Lips. excursor., 1838, p. 119 (cf. Dörfler, Herb. normale, No. 4537).
The strongly hairy specimens of *Succisa* growing in the grass-
sward on the coastal cliffs of the Lizard peninsula (Kynance Cove,
etc.) may be referred to the above variety.

COMPOSITÆ.

Erigeron borealis (Vierhapper) Simmons. Syn. *E. alpinus* auct.
brit.; *Trimorpha borealis* Vierhapper, Beih. Botan. Centralbl., 19,
2. Abt. 1906, p. 447.
According to Vierhapper's monograph of the alpine species of
Erigeron the Scottish and northern plant usually named *E. alpinus*
is not the true alpine species, but another separate species. It
differs from *E. alpinus* in the obtuse basal leaves, the rather
sparingly hairy base of the stem and the strongly hairy, often purple
phyllaries.

Sonchus oleraceus L. var. *albescens* Neuman (Sundsvalls Almänna
Läroverks aarsredogörelse, 1889). cf. Neuman, Sveriges Flora,
1901, p. 57, and Ostenfeld, in Botan. Tidsskrift, vol. 29, 1909, p. 328.
In 1889 L. M. Neuman pointed out that besides the yellow-
flowered typical *S. oleraceus* a form with paler flower occurred in
Denmark. I myself have seen this form in many places in Denmark
and also elsewhere, and during the excursion I found it in Ireland,
at Galway City, where the typical form was also present (the latter
was noticed again at Cork). I think the variety will be found to
occur over the whole of the British Isles.
In Denmark I have cultivated the pale-flowered form and found
that it keeps quite constant. The corollas are really white with a
grey-lilac stripe on the underside, but as the pollen is orange-yellow,
it gives a pale-yellow tint to the whole capitulum, and a closer
examination is necessary to discover how the matter really stands.

ERICACEÆ.

Erica Mackayi Hook. × *tetralix* L.=*E. Praegeri* nov. hybr.
Much has been written about the peculiar *E. Mackayi* Hook.
and it has been considered a hybrid, but I think that Macfarlane
(Trans. Bot. Soc., Edinburgh, Vol. XIX, 1891, p. 58-64) has fully
shown that it is a separate form derived from *E. tetralix*, of which
he makes it a sub-species. I think I have found another argument
which supports the idea of *E. Mackayi* being a true species and not
a hybrid—undoubtedly very near to *E. tetralix* and perhaps to be
considered as a mutant of it. This argument is the existence of

what is apparently a hybrid between *Mackayi* and *tetralix*. The leaves of the true *E. tetralix* are hairy (downy) on the upper side quite apart from the long gland-tipped hairs on their edges which make them ciliate. The flower-stalks, the sepals and the upper parts of the stems are also downy or tomentose, and the ovary is densely hairy. All these characteristics are expressions, according to my view, of only one character, *viz.*, hairiness (tomentum); and this character is absent in *E. Mackayi* which has only the glandular hairs (also present in *E. tetralix*). Consequently in *E. Mackayi* the upper sides of the leaves, the sepals and the ovaries, are glabrous, while the flower-stalks and the upper part of the stem are glandular. Besides this character, the two species differ from each other in the shapes of the corolla and of the leaves. Both produce ripe seeds.

When collecting both *E. Mackayi* and *E. tetralix* on Craigga More near Roundstone (Co. Galway), I was struck with some individuals which did not answer well to either of the two species, and now having examined the material brought home, I feel convinced that we have here a hybrid between the two species. As far as I remember it was not rare at the place (I have three col-lection numbers) and it shows in that respect a parallelism to the fairly abundant occurrence of *E. Watsoni* Benth. (*E. ciliaris* L. × *tetralix*) at Perranwell, near Truro (Cornwall) with its two parents.

The hybrid from Craigga More stands in its characters between its supposed parents; it has an ovary which is glabrous with the exception of some hairs on the ridges; the leaves are broader than in *E. tetralix*, but much more revolute than in *E. Mackayi*; they are nearly glabrous above, and the tomentum on the upper parts of the stems and on the flower-stalks is not dense as in *E. tetralix*; the outer side of the sepals are only very faintly hairy. I have not succeeded in finding any fully developed ovary containing good seeds; and I suppose the plant to be sterile.

Upon these characters I have based my supposition that the specimens are of hybrid origin and I think it is not possible to determine the question more nearly without making crossing experiments, the only absolutely decisive proof in this matter. I have named it in honour of our excellent guide in Ireland, Mr. R. Lloyd Praeger of Dublin.

GENTIANACEÆ.

Gentiana campestris L.

The sub-sp. *germanica* (Froel.) Murb. (the common British plant I suppose) was found near Dunkeld, Perthshire.

The sub-sp. *baltica* Murb. (pro-specie) was found at Southport (golf-links on the dunes) and at Ballyvaghan, Co. Clare.

Gentiana amarella L.

All the plants seen belong to sub-sp. *axillaris* (Schmidt) Muzb., *viz.*, those from Ireland: Ballyvaghan, Co. Clare; England: Butser Hill, W. Sussex; Kingley Vale, W. Sussex; Haweswater near Silverdale, Lancashire; Southport, golf-links.

SCROPHULARIACEÆ.

Alectorolophus (*Rhinanthus*) *minor* (Ehrh.) Wimm. and Grab.

When studying the segregates of *Alect. minor* in northern

Europe, I have found that hardly any of them deserve to be taken as separate species. Most of them are, at least in the northern and north-western parts of Europe, merely variations caused by external conditions ("Standortsmodifikationen" of the Germans) and not hereditary varieties. One of the few variations of somewhat higher value is var. *Drummond-Hayi* B. White, which we saw on Ben Lawers.

The seasonal variations seem not to be fixed in this genus as far as *A. minor* is concerned; hence I take *A. stenophyllus* only as representing the late flowering individuals of *A. minor* sensu stricto (we saw it at Ballyvaghan, Co. Clare), and *A. monticola* only as the late flowering individuals of a small mountain-inhabiting *A. minor*, of which *A. rusticulus* is the extreme. The name *A. borealis* merely represents larger individuals of *A. minor* var. *Drummond-Hayi*.

Some years ago (Botan. Notiser, 1904) I showed that in Great Britain *A. major* (Ehrb.) Rchhb. has only been found in Sussex, while the other records belong to the separate species *A. apterus* (Fr.) Ostf., easily distinguished by the wholly or nearly wingless seeds. It has two areas of distribution in Great Britain, one with Yorkshire as centre, and another in east Scotland. Its general area of distribution is from Great Britain through Denmark, North Germany, Norway and Sweden, east-ward to Finland. For several years I have cultivated it and found it keeping all its characteristics and remaining quite distinct from the true *A. major*.

Euphrasia. The British Eyebrights are not easy to keep separate from each other, although we have the valuable monograph by the late Mr. F. Townsend (Journ. of Botany, 1897). In order to obtain as much knowledge about them as possible I collected during the excursion a good many specimens (about thirty different numbers), and have now examined them more closely. The result is that, while some species are easily distinguishable, others are very difficult to name when using Townsend's paper and Wettstein's monograph. I think a study of the British Eyebrights on the spot will alter our views with regard to several of Wettstein's species.

As it may be of some use to know the identifications made by a continental botanist, of some British Euphrasias, I shall enumerate the species which I have collected and the localities for each of them.

E. Rostkoviana Hayne. A few individuals of a small-flowered form was found at Clifden, Co. Galway, growing among members of *E. brevipila* and resembling it closely. This is hardly distinguishable from *E. hirtella* Jord.

E. Vigursii Davey. Specimens agreeing with authentic *E. Vigursii*, presented by Dr. C. C. Vigurs, were found in Cornwall: Mullion Heath, near the Lizard.

E. brevipila Burn. & Gremli. Seems to be common. Dunkeld, Perthshire; Cressbrook Dale, Derbyshire; Clifden, Co. Galway; Dog's Bay near Roundstone, Co. Galway (low, blue-flowered specimens).

E. stricta Host. Ballyvaghan, Co. Clare; both typical and aberrant forms.

E. nemorosa Pers. Seems to be common in England. Silver-dale, Lancashire; Perranwell, Cornwall; Kingley Vale near Chichester, W. Sussex.

E. curta, Fr. A curious, nearly unbranched, dark coloured heather moor plant, with leaves only slightly clothed with stiff hairs,

may be referred to *E. curta*; it was found on Craigga More and Urrisbeg near Roundstone, Co. Galway. Specimens which I have named *E. curta*, var. *glabrescens* Wettst., were taken on the golf-links at Southport and on grassy, chalky ground at Dogs Bay, Co. Galway. Typical *E. curta* was not met with.

E. gracilis Fr. Seems to be common in Scotland and Ireland. Dunkeld and Ben Lawers, Perthshire; Urrisbeg, Co. Galway; Ballyvaghan, Co. Clare.

E. minima Jacq. In a paper on the Flowering Plants of the Færöes (Botany of the Færöes, Vol. III, Copenhagen, 1907), I have (pp. 844-847) published my studies on the small-flowered Euphrasias of the Færöes and Scotland; from the latter country I had ample material at my disposal through the kindness of the late Mr. Townsend and the late Mr. W. H. Beeby. The main result was that the two Scottish species *E. foulaensis* Towns. and *E. scotica* Wettst. (*E. paludosa* Towns.) are not distinct from *E. minima* Jacq., a widely distributed alpine species, and that, consequently, both species have to be sunk and *E. minima* recorded as a British plant. Nevertheless we find in the later lists of British plants (*e.g.*, Druce's list of 1908), both the former species maintained, and further, in 1909 *E. minima* was published in Journ. of Botany as a new English plant without any reference to its occurrence in Scotland. As I had drawn my conclusions from examination of dried material, I was very interested in finding "*E. scotica*" growing in Scotland on Ben Lawers, and an examination of it strengthened my belief in the correctness of taking it as a mere synonym of *E. minima*; I am therefore glad to learn from Druce's paper (New Phyt., l.c. p. 317) that "Professor Wettstein confirms Professor Schroeter's determination of '*Euphrasia scotica*' from Ben Lawers as *E. minima*, an opinion independently arrived at by Dr. Ostenfeld." I hope that *E. foulaensis* will follow *E. scotica* and disappear also.

E. salisburgensis Funck. Ballyvaghan and Kinwarra, Co. Clare, on limestone. The record from Roundstone, Co. Galway, was not confirmed during the excursion, only small *E. gracilis* being found.

Melampyrum vulgatum Pers.

The *Melampyrum pratense* collected during the excursion (Yorkshire, Honley Woods; Killarney, Co. Kerry) belong to the above-named form, not to the true *M. pratense* L. sens. stricto.

F. hians Druce seems to be the yellow-flowered form of *M. vulgatum*, just as *f. aureum* Norman is the yellow-flowered form of the true *M. pratense* L. I do not know if *M. pratense* sens. strict. occurs in the British Isles; it must be looked for in the northern and mountainous parts.

LABIATÆ.

Lamium galeobdolon (L.) Crantz. var. *montanum* (Pers.) Briquet.

In the British Isles *L. galeobdolon* occurs in the same variety: var. *montanum* (Pers.) Briq. (syn. *Galeobdolon luteum* Huds., propter patriam) which is also found in the Alps. In Sweden, Denmark, Germany and the Sudetes and Carpathians another geographical race var. *vulgare* (Pers.) Briquet occurs which seems to have quite a different area of distribution. (Cf. Fl. exsicc. Austro-Hungarica, Nos. 3295 and 3296).

POLYGONACEÆ.

Rumex acetosella L.

The northern form (var. *acetoselloides* Balansa) was found: at Foulshaw Moss near Grange (North Lancashire) and in a sloping grass-field near Greenfield (West Yorkshire), while the plant from near the reservoir of Greenfield was var. *angiocarpus* (Murb.) as were specimens from Perranwell (Cornwall) and Potter Heigham (Norfolk). A plant from the riverside of the Tay at Perth is an *angiocarpus* which verges somewhat into *acetoselloides*.

Rumex obtusifolius L. × *sanguineus* L. (*nemorosus* Schrad.)

This hybrid was also found on the riverbank along the Tay at Perth, as well as in Cressbrook Dale (Derbyshire).

JUNCACEÆ.

Juncus bufonius L. var. *ranarius* (Song. & Perrier).

Druce (l.c. New Phyt., pp. 321 and 327) on the authority of Professor P. Graebner has taken the form growing in the sand-dunes of Southport as a separate species *Juncus ranarius* Song. & Perrier, and he adds that the " monographer of the genus," the late Professor F. Buchenau, held the same view. The latter supposition is hardly correct; in Buchenau's last work his monograph of the Juncaceæ in Engler, das Pflanzenreich (published 1906) we do not find *J. ranarius* as a species, not even as a variety. He has a var. *halophilus* Fernald & Buchenau (Rhodora VI, 1904, p. 39) of which the diagnosis in Das Pflanzenreich, Juncacæ (p. 106) runs as follows: Flores ultimi sæpe approximati. Tepala externa acuta, acutata vel subulato-acutata, fructu fere semper longiora, interna breviora obtusa vel rotundato-obtusa, interdum mucronata, fructum subæquantia ; semina truncata (the localities given are Quebec, north-eastern part of U.S., Sicilia and Catania); and under this variety he says: formæ intermediæ var. *halophili* et *genuini* haud raro occurrunt, præcipue in locis salsis. Pro exemplo: *J. ranarius* Songeon & Perrier : tepala interna fructum subæquantia vel paullo superantia, acuta vel obtusa et semina ovoidea præbet (Ascherson u. Graebner, Synopsis II, 2, 1904, p. 423 [spec.]) From this we must draw the conclusion that the best authority on Juncaceæ, Professor Buchenau did not consider the salt-marsh and sea-coast form of *J. bufonius* as a separate species. And I think he was quite right in his view ; the differences between the typical *J. bufonius* and the *J. ranarius* are only very minute, and it is easy to find specimens in which some characters are of *ranarius* and others of *bufonius* proper. I do not doubt that it will be possible to keep the form true by breeding, but this argument does not satisfy me, as I am sure that in *Junc. bufonius*, as in most of the common and widely distributed species, there are numerous " elementary species " which will all keep true when cultivated. In the present stage of our knowledge we must not use the elementary species as species in the floristic and phytogeographic sense ; we are forced to use higher units as species and to treat elementary species as varieties or perhaps even sub-varieties. We can no more give specific rank to the saline form of *J. bufonius* than we can make a separate species of a glabrate form of an ordinarily hairy species (e.g., *Melandrium album*). The highest value we can give to this form

from the systematic standpoint is that of a variety—var. *ranarius* or var. *halophilus*.

CYPERACEÆ.

Scirpus cæspitosus, L.

In 1897 E. Palla (Ber. Deutsch, Bot. Ges., Vol. 15, pp. 467-471) pointed out that *Scirpus cæspitosus* (his *Trichophorum cæspitosum*) was not a homogeneous species, but consists of two distinct forms, which he considers as two species, viz., *Trichophorum austriacum* Palla and *T. germanicum* Palla. The more important distinctive marks are anatomical, but external differences also exist. The author further showed that the two forms inhabit quite different geographical areas, *T. austriacum* being a northern and alpine species found in Greenland, North America, the Himalaya, Northern Europe and the central European mountains, while *T. germanicum* was confined to the North German plain, the German "Mittelgebirge," the French plain, Scotland and the South-Scandinavian plain.

In 1903 Ascherson and Graebner (Synopsis d. mitteleurop. Flora II, 2 p. 300) united Palla's two species under *S. cæspitosus* as two " Rassen " (races or varieties); and I think this is the natural way to treat them. I give the following external characters of the two varieties mainly from their description.

S. cæspitosus L. var. *germanicus* (Palla) Aschs. and Graebn. A rather slender form. The mouth of the uppermost sheath opposite the blade rather deeply cut (up to more than 3 mm.), with rather broad, mostly red-coloured and loosely appressed membranous margins. Spikes rather large, many flowered. Bristles of the perigonium papillose at the top. The older sheaths covering the bases of the shoots hardly shining, pale-brownish, often dark from decaying matter.

S. cæspitosus L. var. *austriacus* (Palla) Aschs. and Graebn. A coarser form. The mouth of the uppermost sheath not deeply cut (mostly not more than 1 mm.), with narrow, whitish or pale-brownish, closely appressed membranous margin. Spikes rather small, few-flowered. Bristles of the perigonium mostly not papillose at the top. The older sheaths larger and more loosely arranged, bright pale-brown, shining.

With regard to their geographical distribution the authors have not much to add to that already given by Palla ; they quote only var. *germanicus* from the British Isles.

As it seemed to me to be of interest to know a little more about the distribution of these two varieties in the British Isles I collected during the excursion specimens in four different parts of the British Isles. The result of an external examination was :—

Var. *germanicus*. Ireland, Co. Galway, Craigga More; England Hampshire, New Forest. To these may be added : Hebrides Stornoway (O. Paulsen, 1905), specimens in our Herbarium in Copenhagen.

Var. *austriacus*. England, North Lancashire, Meachop Moss near Grange ; Scotland, Perthshire, Ben Lawers (a form somewhat approaching to var. *germanicus*).

These few localities seem to suggest a rather interesting distribution within the British Isles, but much more abundant material

is necessary in order to come to a decision upon that point. I should like to suggest to British botanists an examination of the material in the large British herbaria (anatomical examination would also be required) in order that the distribution may be better known. Provisionally I should think that var. *austriacus* is confined to the moors (mostly *Eriophorum*-moors) of north England and Scotland, while var. *germanicus* is the common form of the British Isles, at least in the southern and western parts.

In Denmark we have both varieties, but var. *austriacus* is rather rare and occurs almost only in deep *Sphagnum*-moors, while the common form, var. *germanicus*, often grows in drier localities (heaths, etc.)

As to their general distribution I have seen specimens of var. *austriacus* from North America, Greenland, Iceland, Scotland and North England, Scandinavia, Denmark, Russia, East-Prussia, Silesia, Bavaria, and the other mountainous central-European countries, and of var. *germanicus* from the German plain, the French plain, Denmark, West-Norway (?), England and Ireland, the Hebrides and Færöes (where also specimens occur which approach the other variety). Thus the latter has a much more restricted geographical area than the former.

I have omitted to mention the anatomical distinctions as I have not had time to examine my material in that direction, and may refer to Palla's paper quoted above.

GRAMINEÆ.

Arundo phragmites L.

During our visit to the Norfolk Broads the giant form of *Arundo phragmites* growing especially in Surlingham Broad attracted our attention; the leaves of the flowering stems were about 4 cm. broad. As far as I am able to find out by examination of my material this form comes very near to the southern race of *Arundo*: *A. isiaca* Del. (*Phragmites gigantea* Gay, *P. altissima* Mabille) which is common in the Mediterranean region; but the latter has mostly brownish, not dark-violet, spikelets. Ascherson and Graebner (Synopsis II, 1, p. 330) mention a var. *pseudodonax* Rabenh., of which I have not seen specimens, but which, according to the description, answers fairly well to the Norfolk form. It would be interesting to learn, if we really have a special (southern?) form here, or only giant specimens of the common plant, caused by the favourable conditions of growth.

Poa trivialis L. var. *subalpina* Beck (Fl. N. Oesterreich, 1890, p. 86).

Along old watercourses on Crossfell (Cumberland) and, as far as I remember, also on Ben Lawers (Perthshire) we found an interesting small form of *P. trivialis* growing among mosses. The panicle is tinged with violet and rather small; the stolons are not, as ordinarily, borne above the surface, but are buried in the mosses.

I think it may be identified with the above quoted var. *subalpina* Beck, which has the following description: blade of the uppermost stem-leaves very short, not reaching the panicle; spikelets more or less violet-tinged; grows in springy ("quelligen") places (1200 m. alt.)

Triticum litorale Host. (=*Agropyrum pungens* auctt., non *T. pungens* Pers.)

Duval-Jouve has shown that *T. pungens* Pers. is the hybrid between *T. junceum* and *T. repens*, and therefore the British plant, usually named *Agropyrum pungens* R. and S. must bear the name *T. litorale* Host. It is a very characteristic species growing on rather old beaches where the soil is not bare sand, but somewhat clayey. I have never seen it on the Danish coasts and I doubt if it reaches as far north; with us it is replaced by saline forms of *T. repens* L. (*T. litoreum* Schum., etc.) and the polymorphous hybrid *T. junceum* × *repens*.

We saw *T. litorale* in great quantities at Blakeney Point (Norfolk) and at different places near Portsmoth (Hayling Isl.) and along Southampton Waters. At Blakeney Point and Calshot (Southampton Water) the hybrid *T. junceum* × *litorale* was also present, and at the first place perhaps also the hybrid *T. litorale* × *repens*.

POTAMOGETONACÆ.

Potamogeton perfoliatus, var. *lanceolatus* Blytt.

Perthshire, Loch of the Lows and Butterston Loch near Dunkeld.

The form found in these two Scottish lochs answers well to the var. *lanceolatus* Blytt, described from Norway.

POLYPODIACEÆ.

Polystichum lobatum (Sw) var. *Plukenetic* (Lois.)

Ireland, Ballyvaghan (Glen Thna Mountain), limestone.

The well known authority on Ferns, Mr. Christensen of Copenhagen, has determined a curious form of *P. lobatum*, which superficially resembles *P. lonchitis* Roth, as given above; it is the same as Mr. Druce (l.c. New Phyt., Vol. X, p. 323) names *P. aculeatum* Roth var. *lonchitoides* Deakin.

The same authority considers the dubious form of *Asplenium* from Kynance Cove, the Lizard, referred to in Druce's list as true *Asplenium adiantum nigrum* L.

SALVINIACEÆ.

Azolla filiculoides Lam., with ripe microsporangia.

The *Azolla* growing in abundance and fruiting in a little pond near a garden at Woodbastwick, E. Norfolk, is *A. filiculoides* Lam., not *A. caroliniana* Willd. as stated in Druce's notes (New Phyt., Vol. X, p. 324).[1]

A. filiculoides is a species of American origin (mostly South-American) and it was introduced to Europe a long time ago; it is now quite naturalized in West France (Cherbourg, Bordeaux, etc.)

From *A. caroliniana* it differs in the more racemose branching of the fronds (not repeatedly pseudo-dichotomous) and the unicellular hairs on the upper surface of the upper leaves, as well as in microscopical characters which furnish a better distinction.

[1] As I did not collect the plant we saw in a pond near Queenstown Junction, Cork, I do not know if it is *A. caroliniana* or *A. filiculoides*.

NOTE ON SOME NUCLEI FOUND IN GRASSES.

By JESSIE S. BAYLISS, D.Sc. (Birm.),

(Lecturer and Demonstrator in Botany in the University

of Birmingham).

IN the course of an investigation of fungi causing " Fairy Rings " in fields, I have examined very many sections of the rhizomes of healthy grasses for comparison with infected ones, and have been impressed by the extremely elongated form of the nuclei which occur in the steles but never in the cortex or pith.   Most of them were vermiform or curved rather than straight, and a few were apparently bifurcate (*a*) at one end; they were 20 or 25 times longer than their diameter (*b*, *c*).

In *Bromus mollis* very many of them had a length of 22μ and others were as long as 47μ and even 52μ, while the narrow diameter only 2μ.

They are evidently of general occurrence in grasses, since they were found in the rhizomes and flowering haulms of *Triticum caninum, T. repens, Poa pratensis, Dactylus glomerata, Agrostis vulgaris, Lolium perenne, Cynosurus cristatus, Bromus mollis, B. gigantens, Festuca elatior, Hordeum jubatum* and *Alopecurus pratensis.*

They were only to be seen in the actively growing tissue at the bases of the internodes.

Since I have found no reference to such elongated nuclei in any botanical literature I thought it might be well to draw attention to them by means of this note.
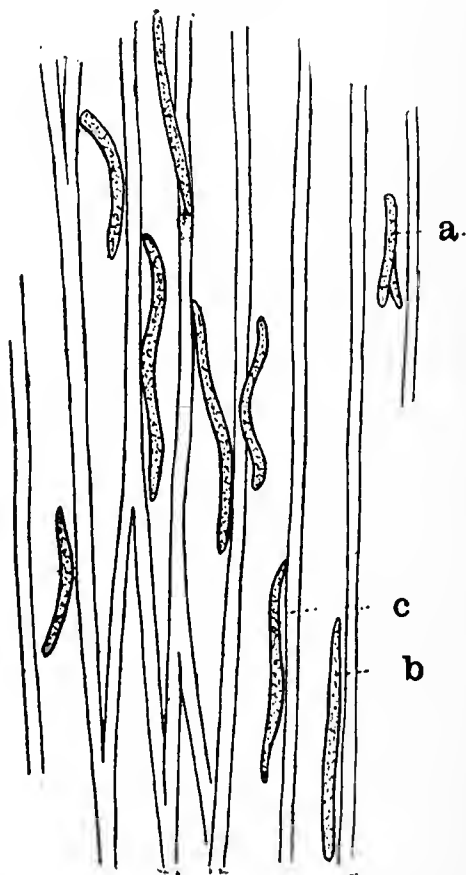
Longitudinal section of a flowering haulm of *Bromus mollis* showing elongated nuclei.   ×800.   (*a*), nucleus with apparent bifurcate end; (*b* and *c*,) elongated nuclei.

A SHORT REVIEW of the GENERAL CHARACTERISTICS AND CYTOLOGICAL PHENOMENA of the UREDINEÆ,

WITH

NOTES ON A VARIATION IN THE PROMYCELIUM OF

COLEOSPORIUM PULSATILLÆ (STR.)

By JAMES R. WEIR.

THE Uredineæ comprise a large group of parasitic fungi, of somewhat doubtful affinities. That they are closely related to the Basidiomycetes will be pointed out during the progress of this paper and their possible relation to the Rhodophyceæ will be indicated. The Uredineæ are characterized by a lack of an evident sexual generation, by the number of different kinds of asexual spores they produce and by their heterœcious habit. The mycelium unlike some of the other parasitic fungi is always found within the tissue of the host plant deriving its nourishment by means of haustoria sent into the host-cells.

The fruiting of the fungus is characterized by the production of a variety of spores, typical of the season in which they are produced, also by the fact that the spores are often incapable of producing infection unless they be transported to a different host-plant. The spores typical of the late stages in the life-history are known as teleutospores. [It is the ultimate condition always present.] They are found in sori and are usually tough-coated resistant spores as they furnish the chief means of tiding the fungus through the winter condition. They are popularly spoken of as winter spores. These spores lie dormant throughout the winter and in the spring germinate to form spores which on the proper host will produce new infection.

The stage of the rust arising from this infection produces its spores as conidia in cluster cups, and for many years botanists regarded this as a separate and distinct fungal species. This stage is known as the æcidial stage. The æcidiospores are produced in great numbers and greatly spread the infection. These spores will not produce infection unless they reach the proper host-plant when they give rise to the next stage characterized by the production of uredospores, the so-called summer spores. This same mycelium during the latter part of its course produces the teleutospores. It

often happens that the æcidia and uredomycelia produce a second crop of spores.

The significance of the two kinds of conidia spores has caused some discussion. Arthur has suggested that in the æcidium the rejuvenescence of the fungus takes place, and in the light of the nature of the æcidium as revealed by the investigations of Blackman and Christman his point seems well founded. It happens in many species that certain of the spore-forms are suppressed, and the life-cycle is much simplified. In some cases the uredospores are wanting, the æcidium being the repeating generation. In cycles with the æcidium suppressed the uredo is the repeating generation. When both æcidium and uredo are wanting the teleutospore is the repeating generation. A complete life-cycle includes all spore forms, the repeating generation being the uredo.

So much having been said concerning the general characteristics of the group we come now to the detailed life-history of a typical form.

A fitting place to begin to trace the life-cycle is with the mature teleutospore, as it is here that the transition from one generation to the other takes place. On germination each cell of the teleutospore gives rise to a four-celled promycelium. The details of this division differ greatly in different species.

In *Phragmidium* a germ-tube is sent out into which the primary fusion nucleus passes. The nucleus by two successive divisions, followed in each case by cell-division, gives rise to the four-celled promycelium (Blackman, Figs. 8, 9). *Coleosporium sonchi arvensis*, the teleutospore divides directly to form the four-celled promycelium which appears as a four-celled structure with the four internal basidia arranged in a chain one above the other (Harper and Holden, Fig. 6). In a study of *Coleosporium pulsatillæ* collected on *Anemone pulsatilla*, the details of the division have been observed to differ from the above in the internal basidia being arranged in the form of a tetrad. This unusual appearance is described in another part of this paper. The essential features being, however, in the division mentioned above that from the teleutospore a four-celled structure is derived, each cell of which bears a single nucleus. From each cell of the promycelium a single spore is produced. This spore is usually uninucleate, but occasionally the nucleus undergoes a division giving rise to a binucleate spore. No cases have been reported in which a wall formation follows this division.

The sporidia on germination give rise to a mycelium the cells

of which are always uninucleate. The stage of the rust resulting from infection by these spores is always characterized by the production of æcidial spores and spermogonia. These cells are produced therefore from a uninucleate mycelium, as first pointed out by Sapin-Trouffy.

The structure of the spermatia causes little difficulty as they are single uninucleated cells. Their function however has not been clearly understood and as it does not enter into the life-history it will be discussed later. The æcidiospores however, are not so simple in their origin and the nature of the æcidium must be given in more detail. The æcidiospores are formed from a mycelium, the cells of which are uninucleated, but the æcidiospores are developed as conidia from a large basal cell which has commonly been spoken of as a basidium. The basidium is binucleated and is the first cell of the binucleated generation. Its origin will be given in detail in another connection. The two nuclei of the basidium divide by conjugate or simultaneous division and after the daughter nuclei have moved apart cell-division follows, cutting off a cell at the top, the æcidiospore mother-cell. The nuclei move apart in such a way that the two nuclei in each resulting cell are never sisters. Immediately following this division the nuclei of the æcidiospore mother-cell divide more apart and cell-division follows, cutting off a very small cell at the lower end, known as the intercalary cell. This soon loses its identity and the æcidiospore rounds up and is free. These binucleated spores give rise to the generation of the rust characterized by having binucleated cells. A division of one of these cells is always preceded by a simultaneous division of the two nuclei and the daughter nuclei which pass to the new cell are never sisters. From this generation of the rust the uredospores and teleutospores are produced.

The uredospores are simple. They are either formed singly on stalks (Blackman, Fig. 78) or in chains (Harper and Holden, Fig. 2), and are always binucleate. They continue this generation of the rust as they always give rise to the mycelium having binucleated cells.

The teleutospore history is far more complex, a young teleutospore is composed of one or more binucleated cells, but these nuclei unlike those in the other spores approach each other and eventually fuse, giving rise to a single large primary fusion nucleus. The mature teleutospore marks then the close of the binucleated generation and the beginning of the uninucleated. The entire life history dropping into two hemicycles.

The life history having been thus briefly stated the special significance of certain phases will now be discussed more in detail.

THE TRANSITION FROM THE UNINUCLEATED TO THE BINUCLEATE GENERATION.

As previously stated the uninucleated condition begins, with the teleutospore and continues until the æcidium is reached, where the transition to the binucleated state is effected. This important condition in the life history escaped the notice of investigators until about ten years ago, when it was first pointed out by Sapin-Trouffy. Although he did not reach the ultimate conclusion of the significance we now attach to all of the details, we must still give him the credit for having placed us on the right road to a complete understanding of the life history of the rusts. It remained for Blackman, and later for Christman ('04), to supplement the work of Sapin-Trouffy by extensive research aimed particularly at the nature of the æcidium and to point out the true nature of the transition.

Blackman in his masterly review of this subject laid especial emphasis on the manner in which the first binucleated cell is produced. Marie had previously held that it originated by a single division of the nucleus of a vegetative cell, that these nuclei were therefore sisters and that they continued to divide by conjugate division until the teleutospore was reached where they fuse. He accordingly placed much more emphasis on the fusion in the teleutospore than he did on the first division which gave rise to a cell with two nuclei.

Blackman's research, however, gives us an entirely new and much more satisfactory method of the origin of the first binucleated cell. He finds that a migration of nuclei takes place into the cells which have first become slightly differentiated and to which he gives the name fertile cells. The migrating nucleus may come from a cell directly below the fertile one in the same filament or from an adjacent cell in a different filament. The two nuclei in a fertile cell are therefore not sisters, and their association in the cells has very much the appearance of a sexual process. He states very positively that this has practically all of the essential characteristics of a true sexual process and he therefore attaches very little significance to the fusion in the teleutospore. In this he is directly opposite to Sapin-Trouffy who regarded the fusion in the teleutospore as a sexual process.

Christman ('05) confirms the work of Blackman as to the association of nuclei but differs very much as to the details. He finds that the fertile cell bearing two nuclei is the result of a conjugation of two previously differentiated gametes and his figures seem very conclusive (Christman, Figs. 1-8). He also agrees with Blackman in regarding this as a sexual process. The result of the research of these two investigators has been to place the sexuality of the rusts beyond further question.

This brings us to some interesting observations concerning the nature of the mycelium of this generation. If the æcidium is to be regarded as a collection of female sexual organs, then the mycelium which produced it is a gametophyte. Since the spermogonia and the æcidia are produced in the same mycelium then we have further reason for believing that the spermatia are functionless male gametes, a view which hæs been held by many investigators since the earliest time. The nature of the spermatia, however, remains uncertain, as well as the question whether the manner of sexual union in the æcidium is a derived or a primitive one.

THE TRANSITION FROM THE BINUCLEATE TO THE UNINUCLEATE GENERATION.

If we regard the association of nuclei in the æcidium as a complete sexual process, then what importance must we assign to the fusion of the nuclei in the teleutospore ? Blackman has suggested that this fusion is in the nature of the reduction division in the higher plants. He accordingly regards the teleutospore as the analogue of the spore mother-cell. Maire and others have regarded the fusion as the completion of a sexual process which began in the æcidium but has been greatly prolonged. Holden and Harper were inclined toward the view that the fusion in the teleutospore is a sexual process. It seems to me very reasonable that the two nuclei which fuse in the teleutospore simply complete the sexual process and that the mature teleutospore is as Blackman suggested a spore mother-cell. It is therefore the last cell of the sporophyte and the first division of the spore is the analogue of the heterotypic division of the higher plants and that the formation of the promycelium is analogous to the formation of the spore tetrad. These cells then are the first cells of the gametophyte.

There is, therefore, a definite alternation of generations as clearly marked as in any of the higher plants and based on the same essentials, namely the reduction of the number of chromosomes

in the gametophyte. This must remain somewhat problematical, however, as the number of chromosomes cannot be counted for either generation.

Nuclear Division in the Uredineæ.

Nuclear division in most of the cells of the Uredineæ is of an exceedingly simple type. The nuclei according to Blackman (whether single or conjugate) lose their membrane, the nucleolus becomes extruded and the chromatin condensed into one or sometimes two masses. A rudimentary spindle is sometimes formed and on this the chromatin becomes spread and is drawn apart into two or sometimes four pear-shaped masses which separate and form the daughter nuclei. In the paired nuclei of the sporophyte generation the stages of the division of the two nuclei are the same at all times in any given cell. This method of division is to be regarded as amitotic or, at least, a very greatly reduced form of karyokinesis.

In the promycelium the two divisions are much more typical and compare closely with that which prevails in the higher fungi and algæ and even in the higher plants. The work of Harper and Holden is probably the most exhaustive that has been accomplished so far in this field of research and their results will be given somewhat in detail.

The resulting fusion nucleus is nearly spherical and occupies a position near the centre of the cell. The chromatin is arranged in rather dense masses. The first evident change which the fusion nucleus undergoes is a loosening up of the dense chromatin masses. The threads become definite in outline and are more readily traced (Fig. 13). Next they increase in thickness and sharpness of outline This is probably due to a shortening of the thread. Closely following this stage the nuclear membrane disappears and the spirem lies in a finely granular substance not sharply distinguished from the surrounding cytoplasm. The thread is seen now to have split longitudinally and in certain parts the daughter segments diverge widely while in others they are closely applied (Fig. 17). This phenomenon of the nucleus is rather interesting as it establishes a point of similarity in this division and the first or heterotypic division of the higher plants. The spirem now segments transversely into several pieces which later become arranged on the spindle as in more typical cases of mitosis.

The stages in the formation of the spindle were not observed

by Harper and Holden. However, they have observed and figured the equatorial plate stage giving a characteristic and interesting figure (Fig. 19). All of the characteristic structural features of this stage in algæ and fungi generally are present, polar radiations, chromosomes, central bodies and spindles are all sharply differentiated.

The chromosomes are rather irregular and are never found in a flat plate as in the typical mitotic figure, but are always more or less strung out along the spindle (Figs. 18 and 19). The passage to to the pole is also somewhat irregular. The daughter nuclei are organized and cell-division follows, almost immediately. Following cell-division the two daughter nuclei enter the prophase of the second division. This stage seems to be essentially the same as that of the first, but the figures are so small that they are difficult to observe with certainty. Following the second division, cell-division takes place and the tetrad division is complete. In comparing this with the tetrad division of the spore mother-cells of higher plants it may also be cited that the four cells produced are essentially spores, as they often fall apart and give rise to the new mycelia, usually, however, their growth is arrested and the sporidia are formed. The name promycelium is therefore seen to be somewhat misleading.

Variations in the Promycelium of *COLEOSPORIUM PULSATILLÆ* (Str.).

In all the forms of rusts reported so far, there seems to be a uniformity in the production of the promycelial cells, each cell of the germinating teleutospore gives rise to a four-celled structure, the cells of which are borne one above the other forming a structure in the nature of a filament. During the study of several rusts collected on various species of *Compositæ* and *Ranunculaceæ* growing in the English Garden at Munich, the observation was made that certain variations from this typical condition seemed to have occurred in a species of *Coleosporium* which has been identified as *C. pulsatillæ* (Str.) growing on *Anemone pulsatilla*. I am in no wise sure that this variation is expected to occur frequently in the sori of this rust; since I have observed it only in the case here mentioned, I think it is not, and must be regarded as an abnormality or as an occasional variation.[1] It seems to be of sufficient importance, however, to justify the present report. In the following paragraphs

[1] The same variation has been noted on a collection of *Coleosporium* sp. growing on *Vernonia noveboracensis* (Willd.) in the campus at Indiana University during the fall of 1906.

the main points of my study will be presented. The material was for the most part collected during the summer of last year.

METHODS.

The material used was fixed chiefly by placing it for twenty-four hours in Flemming's stronger solution, nearly all material was fixed in the field. Specimens were also brought into the laboratory for germination experiments. After fixing, the material was then washed in running water for several hours, dehydrated, passed through chloroform and then embedded in the usual manner. For staining, Flemming's triple stain was used.

By keeping the teleutospore material in a cooling chamber, the germinating power was retained for several weeks. If the leaves with the masses of teleutospores are placed on well saturated filter paper under a bell jar at a temperature of 20°C, germination takes place very readily. Such cultures made in the evening always produced on the following morning abundant sporidia. At ordinary room temperature the teleutospores germinated freely, the sori losing their waxy appearance and under the s. m. showed as spongy masses due to the growth of the germ tubes. The germinating experiments were also conducted in hanging drop cultures in Vantugam cells.

THE TELEUTOSPORE.

The teleutospores appeared through the greater part of the fall, and are found in dense rounded or oblong orange yellow sori, sometimes almost covering the entire under surface of the leaf. The young spore is always a single cell and contains two nuclei, the result of a division of a pair of nuclei in the mother cell. The spore possesses a delicate exosporium, which has more of the appearance of a plasma membrane than a spore wall. Usually the spore about doubles in volume. The nucleus becomes very large and about this time the young spore is cut off from the mycelial cell by a cross wall. The nuclei increase in size, at the same time approach each other and begin to fuse. At this stage the nuclei seem to become more granular or open. The chromatin threads are spread more uniformly about the nucleoli and are characterized by a much smoother outline than they possessed in the former conjugate stage. When the two nuclei come together the nuclear membrane at the point of contact disappears, and finally no line of separation can be distinguished. They continue to fuse until the entire membrane is absorbed and we now have a single large round nuclear mass. After fusion the teleutospore is stimulated to growth at once, and forms the promycelium.

THE FORMATION OF THE PROMYCELIUM.

According to Harper and Holden the fusion nucleus divides and the now elongated teleutospore divides, each daughter cell receiving one of the daughter nuclei. Each daughter nucleus now divides as above and the teleutospore has now grown into a four-celled promycelium, each cell of which contains a single nucleus, the four internal basidia are arranged one above the other and looking like a four-celled spore, each basidium gives rise to a pedicelled two-nucleated spore, the so-called sporidium. This is the usual and typical condition in most of the forms studied (Arthur) (Harper and Holden, Fig. 6). In *Coleosporium* sp. on *Vernonia* and on *Anemone*, the latter forming the subject for the present study, the details of the division relative to the formation of the promycelium differ from that of the above in the fact that there seems to be an occasional variation in the formation of the internal basidia, being arranged in the form of a tetrad. It was first thought that such a condition was due to accidental displacement or something of the sort, but after a careful study of many stained and free mounted preparations it seemed that there was undoubtedly a tetrad formation of the promycelium. The appearance was noted alongside of the usual four-celled superimposed condition, and in the numerous preparations I have made, the tetrad appearance occurred most frequently at the inner edge of the sori in the angle formed by the branching of the mid-rib. In the hanging drop cultures where displacement or crowding would be impossible, the tetrad was observed and it germinated in the usual way, each cell sending out a single germ tube on the end of which is produced a sporidium and a promycelial nucleus passes out into each sporidium. Mounts from the germinating material from the cultures on the filter paper, made by removing with a needle a sorus with a bit of the epidermis and placed on a slide without cover glass, showed in one instance not only the typical promycelium but the tetrad in various stages of germination also. The two terminal cells had just begun to send out tubes, the nuclei becoming elongated and pointing toward the opening of the tubes. In another instance only one of the two lower cells had germinated. In one hanging drop culture a perfect tetrad with all four cells in a germinating condition furnished the most striking instance. At first the sporidium is uninucleate but its nucleus divides and since no cell-wall is formed, we have a binucleated sporidium.

THE UREDOSPORES.

The Uredospore material was abundant throughout the later part of the summer and was found along with the teleutospores up to the time of frost. My own observations on the process of spore formation in those forms agree in the main with that reported by Harper and Holden. The two nuclei at first lie in the long axis of the cell but are finally side by side in the transverse axis when they both divide simultaneously. The division always results in the cutting off in the daughter cells of a pair of nuclei. The two nuclei come one from each of the mother nuclei of the mother cell so that the nuclei in each cell are not sister nuclei. The next division is somewhat different, the upper cell divides unequally, a lower cell is cut off obliquely and is much smaller and becomes sterile and finally disappears, while the upper cell becomes the uredospore. Harper and Holden have suggested that in reality this spore is an æcidiospore, but in the light of the research of Sapin-Trouffy, Blackman and others, whose work was aimed particularly at the nature of the æcidium, it seems that they answer more nearly to the nature of a typical uredospore with the exception that they are borne as conidia and not in the usual manner. This exception seems then to be superficial rather than real, as æcidio-spores are always produced from uninucleated hyphæ while the uredospores come always from binucleated hyphæ as is the case here.

HAUSTORIA.

The haustoria as in *Coleosporium sonchi-arvensis* are normally binucleated; whether the haustoria were on the ends of the hyphæ cells or were formed farther back on the hyphæ, I was unable to determine. They were usually rounded in form and presented a granular appearance. The nuclei were observed to be very near each other in some cases in contact. The former condition is characteristic for the conjugate nuclei; the latter condition was due in all probability to the sectioning.

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"NUCLEAR OSMOSIS"

AND ITS ASSUMED RELATION TO NUCLEAR DIVISION,

BY J. BRETLAND FARMER, F.R.S.

THE attempts which have been made within the last thirty years or so to unravel the secrets of the processes accompanying a nuclear division, group themselves rather naturally into two classes. The one, prior in time and more naïve in character, seeks to explain the complex series of changes as the outcome of the operation of correspondingly complex cell-structures. The second and more modern efforts have been in the direction of shewing that the changing configuration of a dividing cell is the expression of the series of chemical reactions which are conditioned and limited by the ultimate physical structure of the protoplasm in which they occur. Unfortunately our knowledge both of the reactions and of the conditions is extremely fragmentary as yet, but it is only by pushing outposts into unexplored ground that new discoveries can be made. It is something to have arrived at a conviction that not in reliance on a *Deus ex machina* does the possible extension of knowledge lie, but rather in investigations on the origin and meaning of the structures themselves.

Of course progress has been slow, but this is the inevitable consequence of attacking problems of so high an order of difficulty. Many mistakes have been made in the past, and many will be made in the future. There is divergence of opinion on matters which

can only be settled by extensive and comparative observation, and as soon as anyone embarks on the perilous path of interpretation he is beset by risks that ever await the pioneer.

Certain guiding principles, however, are slowly emerging from the chaos, and the ancillary sciences of chemistry and physics are now more helpful than formerly. Much has been done to elucidate the behaviour of colloids, and we possess a clearer knowledge of the energy changes that are associated with the chemical and physical transformations within the cells, and we also realise that dimensional considerations are not to be ignored in estimating the effects of forces which are acting within the limits of a single cell.

It may be freely admitted that we are certainly not in a position to furnish anything like a full and satisfactory explanation of the features which characterise the progress of a nuclear division. But if we are to wait until we can offer a full solution of the problems involved, we may as well abandon the enquiry at once. We are obviously bound to go on, and therefore any serious attempt to frame even a working hypothesis, to say nothing of a complete explanation, is entitled to consideration.

Dr. Lawson, in two memoirs published by the Royal Society of Edinburgh,[1] has attempted an extensive explanation of, at any rate, some of the problems of mitosis, and it is the purpose of this communication to endeavour to weigh the merits of his contribution. The earlier memoir mainly deals with the stage known as synapsis, and Dr. Lawson feels himself justified in concluding that the common impression is that this stage is associated by a *contraction* of the chromatin is erroneous, but that the significance of the stage is open to more reasonable interpretation, *viz.*, that the nucleus is greatly enlarging and is acting as a sap vacuole.

Dealing in the first place with the view that the generally admitted idea of contraction is erroneous, it is not improbable that many workers will continue to find some difficulty in accepting Dr. Lawson's conclusions, and it must be confessed that he has not, on his side, rendered agreement too easy.

A critical study of his own figures convincingly proves that, even in the object selected by Dr. Lawson himself, a contraction of the chromatin-containing mass clearly occurs during synapsis. This is shown by the method of tracing, and also by calculation

[1] The phase of the nucleus known synapsis, *Trans. Roy. Soc. Ed.*, Vol. XLVII, p. 591, 1911.

Nuclear Osmosis as a factor in mitosis. *Trans. Roy. Soc. Ed.*, Vol. XLVIII, p. 137, 1911.

based on the diameters actually figured. Thus as nearly as could be measured, the diameters of the mass taken as a sphere, shewn Figs. 1, 7 and 13, are respectively 24, 22 and 20 mm. The *volume* of the respective spheres occupied by the chromatin works out at 7238, 5575 and 4190 cub. millimetres. That is to say a shrinkage occurs of about 43% as between the presynaptic stage of Fig. 1 and the synapsis stage stage of Fig. 13.

Naturally it is difficult to obtain very accurate measurements, but the results just given are not discordant with the views more generally held on the existence of contraction as might have been anticipated on mere *linear* measurements.

The increase in the size of the nucleus has, of course, been noted by other observers, and the author is probably correct in attributing it to an increase of nuclear sap resulting from higher osmotic tension. It is less easy to follow him in his view as to the *direction to which this pressure* is assumed to act, for surely it must act equally in all directions, although differences of surface tension may and will determine the actual form assumed by the nucleus. The hypothesis as to the supposed relation between the directive extension of the nuclear vacuole and the rounding off of the the individual spore mother-cell, appears to need further explanation than is accorded to it.

It is not improbable that many investigators who are familiar with the facts of mitosis, in so far at least as they can be ascertained by observation, may find themselves unable to share Dr. Lawson's conviction that " Nuclear osmosis " is to be regarded as a satisfactory explanation of the complex mechanism commonly known as the achromatic spindle. Dr. Lawson, after his friendly criticism of a paper of which the present writer is a joint author, will not misunderstand the situation if the points in which his own hypothesis appears to be defective are rather frankly examined. For it is only by fair discussion that the meaning of the facts is likely to be elucidated. It is not the writer's intention to defend here and at length the thesis that electrical conditions, resulting from chemical changes occurring in the peculiar physical substances of which the cell is composed, are responsible for the structures in question. But it must be pointed out that Dr. Lawson seems to under-rate the circumstance that electrical disturbance is a very common and a very easily ascertained *fact* in many phases of cellular activity, that the forces concerned are or may be of considerable magnitude having regard to the limited space in which

they act, and finally that, with our growing knowledge of the physics of colloids, many reactions and dissociations which would have appeared impossible a few years ago, are now recognised as not only possible, but are actually known to occur at the same time. The writer, still holds that " the time has not yet arrived when it will be possible to give an explantation of these cellular changes that will prove completely[1] satisfactory from a physical point of view."

Obviously this must continue to be true until we know a great deal more about the nature of protoplasm and the dissociations and other changes that go on within its substance. But it seems absurd to compare, as Dr. Lawson does, a working hypothesis, however incomplete, but based on electrical conditions of which we do know something, with mystical notions on " cell polarity " of which, as an efficient cause, we know absolutely nothing.

Dr. Lawson's own working hypothesis seems to be somewhat as follows. The nuclear cavity really represents a vacuole filled with sap as well as with other solid matter, chromatin and the like. The vacuole is contained in a semi-permeable membrane (the author continually calls it a *permeable* membrane, but this is perhaps a slip, as, of course, semi-permeability is of the essence of an osmotic system). The extra nuclear protoplasmic " reticulum " is continuous, with the nuclear wall, which itself is supposed to be of cytoplasmic origin. Contraction of the nuclear cavity (vacuole) at and after diakinesis produces a strain in the continuous cytoplasmic reticulum (which seems to be assumed to represent a permanent structural differentiation), and this contraction is thus held to be responsible for the first appearance of the spindle fibres. As the vacuole continues to contract, the fibres become more and more pronounced owing to the tension supposed to be thereby developed in the reticulum, and finally each chromosome becomes separately enveloped in the infolding vacuole wall.   In this way, it is believed, each of these bodies comes to possess its own sheath of fibres. The result is that, instead of a single osmotic system represented in the nucleus, we now have established as many independent " osmotic systems " as there are chromosomes.

Dr. Lawson considers that the nucleus before its period of contraction occupies a cubic capacity of about half that of the cell, and since part of his argument as to the striking effect of the con-

[1] Dr. Lawson, doubtless by inadvertence, omitted the word "completely" when quoting the above passage, thereby altering the sense of the original in no small degree."

traction is based upon this volume relations, it is worth while to check it. An examination of his own figures shews, however, that the space occupied by the nucleus is only about *one quarter* of the of the volume instead of the half assumed by the author.

But apart from this circumstance, Dr. Lawson's whole hypothesis bristles with difficulties with which he has not himself dealt. For if the contraction of the *nuclear* vacuole can bring such structures as spindle fibres into existence, why cannot the same effect be produced by ordinary plasmolysis of the cell ? This operation can be very rapidly carried out, but no appearance suggesting spindle formation ever results. Again, why is the spindle polarised at all on the assumption of a central contracting vacuole as the determining factor of its existence ? How can such a vacuole be held responsible for such a structure as may be observed during the mitosis of a germinating spore of *Pellia* for example, or for the equally diagrammatic figures of many animal cells ? It would seem to be impossible, without piling up an overwhelming load of accessory hypotheses to bring all these examples into line by attributing to all and every one of them a common origin in forces supposed to be exerted by a centrally contracting nuclear vacuole.

Furthermore, a closer scrutiny of the manner in which each chromosome is believed by Dr. Lawson to become severally enveloped by a portion of the nuclear membrane, carrying with it a share of the adhering cytoplasmic fibrils, seems to reveal still fresh difficulties. The vacuole membrane is clearly elastic, the actual contour being largely determined by conditions affecting surface tension. The size of the vacuole itself is of course mainly dependant on the relative concentration, within and without it, of osmotically active substances. Now if it be assumed that the contraction is due to permeability of the wall, surface tension alone must be responsible for its final contraction, and it seems impossible to regard each chromosome enveloped separately in its share of the original film as an "osmotic" system " at all.

Furthermore it is difficult to imagine that a membrane possessing the properties thus attributed to it, of sliding over and enveloping the separate individual chromosomes can possible adhere in the way postulated, to the achromatic cytoplasmic reticulum in the first place assumed to exist, and in the second to be drawn out into the fibrillar structures with which everyone is acquainted. If on the other hand it is assumed that a sort of plasmolysis is responsible for the contraction of the nucleus and the subsequent events, one is

faced with difficulties of, if possible, a still higher order. For whence comes the high degree of concentration of osmotically active substance, and why does it not make itself apparent in many other obvious ways, as for example, in a great increase in the size of the cell, which should occur at any rate in animal cells with their tenuous membranes ? Dr. Lawson notes that it is a curious circumstance that somatic mitoses are characterised by " the drawing out of only two conical shaped sheaves of kinoplasm " instead of the multipolar arrangement that often marks the early stages in the meiotic spindles. He attributes the difference to the absence of vacuoles in the cytoplasm of cells in the meiotic phase, and to their presence in the ordinary body cells ; " The numerous vacuoles which are always present in the cytoplasm would render a radial or a multipolar arrangement of the kinoplasm impossible." But he does not attempt to explain the cause of the impossibility, nor is it at all self-evident. Vacuoles are not rigid, immovable things, but in any event one would rather have expected that if they were able to exercise any mechanical influence on spindle formation at all, they would rather have tended to produce than to check the formation of multipolar spindles, inasmuch as they do serve in some degree to partition up the cytoplasm.

As regards the stages of anaphase and telophase the author has not worked out the consequences of his ideas in any detail so they need not be further discussed here. Enough has perhaps been already said to indicate that in the opinion of the present writer a case has not been made out for the acceptance, even as a working hypothesis, of " nuclear osmosis " as a serious factor in mitosis ; and certainly not in the sense that Dr. Lawson claims for it. Any far reaching theory must be applicable to the animal as well as the plant cell, for the essential similarity of the process in the two kingdoms is even more striking when the differences in other respects between the respective cellular conditions are borne in mind.

FLORAL EVOLUTION : WITH PARTICULAR REFERENCE TO THE SYMPETALOUS DICOTYLEDONS.

BY H. F. WERNHAM.

VI.   TETRACYLIDÆ : PART III. TUBIFLORÆ (concluded).

DR. MOSS, in a recent series of lectures on the principles of classification of the Angiosperms,[1] made the remark that the question whether the allied orders of Contortæ, Tubifloræ and Plantaginales have any relationship with Archichlamydeæ, or whether they have diverged from the other sympetalous forms, is the outstanding problem of the Sympetalæ at the present time. The key to the solution of this problem seems to lie in the origin of the Contortæ; and we have endeavoured already in these papers to attack this question, and to find some support for the view that this cohort, like those comprising the Pentacyclidæ, is derived from a polypetalous stock. This once established, the origin of the Tubifloræ will not be far to seek; its connection with Contortæ by way of our so-called "Transitional Group" has been urged in the last chapter. It is the object of the present chapter to add the remaining links in this evolutionary chain by tracing the connection between this last-named group and the higher Tubifloræ—the Personales and Lamiales of Bentham and Hooker—and between the latter and Plantaginales.

The prime distinction between the higher Tubifloræ and the Transitional Group lies in the character of zygomorphy coupled with oligomery of the andrœcium; the regular flower with iso-merous andrœcium is very rare among the members of the groups which we are about to consider. In the latter, as already indicated at the beginning of the last chapter, the fundamental tendencies in respect of economy and adaptation to insect-visits stand fully

[1] Delivered at University College, London University, during Michaelmas Term, 1911.

realised; but the further elaboration of these tendencies will be met with in active progress. Thus the androecium tends, in all the principal families concerned, to be reduced to two stamens only; the structure of the anthers and arrangement of the stamens is frequently specialized in various ways in obvious relation to the pollination-method; the shape and structure of the corolla is diversely elaborated in the same. relation. Further, the progressive specialization of the fruit foreshadowed in the parental apocynal stock (Apocynaceæ, Asclepiadaceæ), and seen also in the Transitional Group (Boraginaceæ), plays a prominent part in the higher Tubifloræ and finds expression in affording critical characters for some of the families. Some indication of this phenomenon and of its significance has been given in the last chapter.

The large majority of the forms which now concern us are herbaceous in habit, as is to be expected in view of their high place in the evolutionary scale (see chapter IV). Notable extensive exceptions to this are afforded by nearly all Bignoniaceæ and many Verbenaceæ. Whether or no the arborescent habit is in these cases significant of relative primitiveness remains to be considered in the sequel.

As being the more closely connected, it would seem, with the Transitional Group, we consider first the group characterized primitively by the presence of an indefinite number of ovules in the ovary, and named in the last chapter.

The Multiovulatæ.

The characters of the families comprised in this group are summarised in the table facing p. 152, and the relations between the two modern accepted systems of classification are indicated as in previous tables. It will be seen that the essential points of difference, beyond those dealt with in the last chapter, are not of any very serious importance; the chief is concerned with the systematic position of Selagineæ, and this will be considered in due course. In Bentham and Hooker's system, moreover, Multiovulatæ and Diovulatæ rank as separate cohorts.

Setting aside for the present the highly specialized Acanthaceæ, a glance at the table will show that the largest family concerned is Scrophulariaceæ; it comprises considerably more species than all the others taken together. These species, again, reveal a wider range of difference in floral structure *inter se* than do those comprised in any of the other families; at the same time they seem to constitute a more or less natural and well-defined group. The sub-

regular flower of *Verbascum* (including about 150 species), together with its short corolla-tube and isomerous andrœcium, links the Scrophulariaceæ closely with the Transitional Group as represented by Solanaceæ; while *Verbascum* is united with the more typical members of its family by way of the genus *Celsia*, generally similar, but with oligomerous andrœcium. The flower of *Verbascum* shews, again, distinct zygomorphy in its unequal and dissimilar filaments. The isomerous andrœcium occurs but rarely in Scrophulariaceæ outside *Verbascum*,—e.g., in the small genera *Scoparia*, *Bacopa*, and sometimes in *Sibthorpia* and *Capraria*; and the total number of species in which this condition obtains represents 7—8% of the gross number contained in the family.

In more than 60% of Scrophulariaceæ the corolla-segments exceed the stamens in number by one—*i.e.*, the latter number four, the posterior stamen being aborted or represented by a staminode (*Pentstemon*); the four stamens are usually arranged didynamously. In the remaining 30% the andrœcium is composed of two fertile stamens only, the other members of a hypothetical pentamerous whorl being, in some cases, replaced by staminodes; these may amount to mere rudiments only, or may be altogether absent (*Calceolaria*, *Veronica*).

It will be convenient to urge at this point with a certain confidence that the homology of the staminodes in the higher Tubifloræ is very probably with the fertile stamens, and that this conclusion is not—at least, in most cases—open to the same objections which we have admitted in the case of the Primulales (chapter III). We cannot discuss this question at length here ; but favourable evidence is not lacking, *e.g.*, in respect of form, position and development, in the progressive degradation of the anthers in certain series of allied forms, and so on.

Payer, in his *Traité d' Organogénie comparée de la Fleur* (Paris, 1857, p. 542), furnishes details of development in the flower of *Lophospermum* (*Maurandia*) *erubescens*, a member of the Antirrhinoideæ-Antirrhineæ section of Scrophulariaceæ. The posterior stamen appears first, then two lateral stamens ; then an anterior pair. The posterior stamen, however, never bears a fertile anther, but persists as a staminode. In this case there seems to be little room for doubt that the staminode is the true homologue of a stamen. In the case of *Veronica speciosa*, however, Payer observed no sign of more than two stamens at any stage of development.

In regard to adaptation for insect-visits, over and above the

fundamental character of zygomorphy which to a greater or less extent is a feature of practically all the species, the Scrophulariaceæ shew considerable diversity. Progressive advance centres, broadly speaking, upon the individual flower rather than upon the inflorescence as a whole ; and herein lies the broad distinction between Tubifloræ and Campanulatæ, a distinction reflected in the two different types of zygomorphy to which we have already drawn attention (chapter I). Close aggregation of flowers is thus relatively rare in the former group, and where it occurs, as in Labiatæ, it is to be regarded as a special rather than a fundamental adaptation ; the case is, of course, the reverse in Campanulatæ, where zygomorphy is to be regarded, in most cases, as the outcome, more or less, of aggregation, as exemplified in Compositæ and Umbelliferæ.

The corolla in Scrophulariaceæ ranges from the open type with short tube characteristic of the tribe Verbasceæ, to long-tubed, bilabiate, spurred, saccate, personate, &c., forms, and the details of pollination have been ascertained in many cases. In some forms the corolla attains a considerable size (*Digitalis, Gerardia, Lamourouxia, Cycnium,* etc, etc.), reflecting the general tendency of the apocynal stock and its descendants towards enlargement of the individual flower for the attainment of conspicuousness.

The carpel-number is almost invariably two, as is the case, ndeed, in all the Multiovulatæ. The flower in the genus *Bowkeria* (with about five species) is tricarpellary, and the same obtains occasionally—probably as an abnormality—among other genera of Scrophulariaceæ. The ovary is nearly always bilocular and multiovulate. In the latter regard an important tendency to reduction in ovule-number is traceable within the family ; this is seen in some species of *Veronica,* in the genera *Melampyrum, Tozzia, Leptorhabdus,* where two ovules only are associated with each carpel, and *Tonella* with one to three ovules ; and the tendency culminates in the tribe Selagineæ, in which a single pendulous ovule occupies each chamber of the bilocular ovary.

We may take the present opportunity to notice briefly the systematic position of this tribe. Its members are all herbaceous or suffruticose and almost exclusively confined to South Africa, a few species occurring also in Madagascar. In Bentham and Hooker's system, and in the chief previous systems, Selagineæ have been ranked as a distinct family, and further, their affinity has been regarded as with Diovulatæ rather than with Multio-

vulatæ. This has doubtless arisen from the presence of but a single ovule in each ovary-cell, in contrast with the multiovulate ovary of the typical "personalian" flower. But the single ovule is pendulous from the apex of the cell, while in the schizocarps of Diovulatæ the ovule is usually erect and basal. There is in Selagineæ no indication of what we have named "schizocarpy" in the last chapter, and to which the uniovulate condition of the ovary-cell in Diovulatæ is due: each loculus corresponds to a carpel, which has therefore one ovule, not two, associated with it. In habit and general facies, again, the Selagineæ appear to be more or less closely linked with some of the smaller-flowered members of Scrophulariaceæ; and it may be urged that this tribe, with its commonly occurring dense clusters and spikes of small flowers, represents a tendency to acquire conspicuousness by the aggregation of florets. Indeed, this tendency finds definite realization in the closely allied family Globulariaceæ, in which the inflorescence is capitate, delimited by an involucre of bracts. This family differs further from the typical Selagineæ in the possession of a unilocular ovary, the solitary ovule being pendulous from the apex. This condition is, however, foreshadowed in Selagineæ, for here the two free achenes are commonly unequal in the fruit, and one is sometimes sterile or obsolete; the ovary in Globulariaceæ is thus probably the result of suppression of one of the carpels.[1]

On the whole the writer is inclined to associate Selagineæ with Globulariaceæ in one family, Selaginaceæ, in agreement with the system of Bentham and Hooker, but in close connection with Scrophulariaceæ, as in Engler's system.

The fruit of Scrophulariaceæ is nearly always a two-celled capsule, revealing no tendency to schizocarpy; and neither fruit nor seeds display any special adaptations for dispersal comparable, at any rate, with those found in certain of the allied families with which we shall have shortly to deal.

The large majority of Scrophulariaceæ are herbaceous in habit, the shrubby and arborescent forms being very few in number; this is, of course, consistent with the very general trend of advance in the higher Sympetalæ. An interesting special tendency in relation to habit is seen in the heterotrophic mode of existence adopted by many of the Rhinanthoideæ (*Euphrasia, Pedicularis,* etc.), which

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[1] See Le Maout and Decaisne. *A General System of Botany, Descriptive and Analytical.* Mrs. Hooker's translation (1873), p. 619.

are hemi-parasites. This tendency is expressed in two allied families, each of which is extremely specialized in habit—the insectivorous Lentibulariaceæ on the one hand, and the totally parasitic Orobanchaceæ on the other.

The Lentibulariaceæ reflect a high degree of advance in floral characters. The corolla is usually strongly zygomorphic, often personate, and with a spur more or less prominently developed. The conspicuous bilabiate stigma is highly specialized; and the numerous ovules are borne on a free-central placenta. The last-named character, as Bentham[1] has pointed out, is foreshadowed in Scrophulariaceæ. He says: " In respect of the former character " (free-central placentation) they (Lentibulariaceæ) come very " near to *Limosella, Lindernia,* and other Gratioleæ, with parallel " dissepiments and entire valves ; for in these plants the dissepi- " ment is very thin, and usually detaches itself from the valves " before maturity, so that being concealed by the seeds, which fill " nearly the whole capsule, it often escapes observation, and many " of these genera have frequently been described as having a " unilocular fruit." The unilocular character of the ovary in Lentibulariaceæ, then, would appear to be secondary, the result in descent of the degradation of an ancestral septum.

In Orobanchaceæ the andrœcium consists of four stamens arranged didynamously. The habit represents the final stage of the parasitic tendency exhibited in Rhinanthoideæ. The most important difference between Orobanchaceæ and Scrophulariaceæ is in the septation of the ovary; in the former family the ovary is unilocular, the numerous ovules being borne upon projecting parietal placentæ. The carpels are nearly always two in number, —only rarely and abnormally three.

This type of unilocular ovary—the result of union of carpellary leaves at the margins only—will be readily distinguished from the type which occurs, *e.g.,* in the Primulaceæ and Lentibulariaceæ, where the unilocular condition results, presumably, from the degradation of septa in the course of descent; this presumption is supported by the free-central character of the placentation. The former type, with parietal placentation, is to be regarded as relatively primitive, as urged in the last chapter; the latter is clearly secondary. The former type, again, is the rare exception among representatives of the stock with which we are concerned, and which we have dealt with so far; thus, in the Transitional

[1] See Lindley, *The Vegetable Kingdom.* 3rd edition, p. 686.

Group the ovary is almost always septate, and in one important branch we have seen (chapter V) that there is a definite tendency to secondary septation. The most noteworthy exception among the Contortæ is afforded by Gentianaceæ; while in the Geraniales Sapindales plexus the ovary is characteristically septate.

In Gentianaceæ the members of one section have flowers with ovary unilocular and placentæ not projecting; in another section the placentæ project; and in a third (Exaceæ) the placentæ appear to meet in the middle, so furnishing a septum. In a group of this kind, in which a progressive series leading from one extreme condition to another is traceable, the problem is to discover which of the two extremes is to be regarded as the relatively primitive condition—in other words, to discover the *direction* of the serial progress from the aspect of evolution. It will appear from the remarks that we have made in the present connection that the progress is from the unseptate to the septate condition; so that in Gentianaceæ, and in other families with which we are immediately to deal, the principle of the ovary-structure is rather to retain unilocularity rather than to acquire it; whereas in the caryophylline stock (chapter III), for example, the case is the reverse. The unilocular, like the septate state may be the result of more than one cause; in the Selaginaceæ-Globulariaceæ group we have lately seen that it is due to the abortion of one of the carpels—a cause very different from either of the two referred to immediately above.

From the closeness of their connection with the Transitional Group, and the considerable diversity of their floral structure, we are led to regard Scrophulariaceæ as a group relatively primitive among the Multiovulatæ. From this family we have already in the present chapter traced certain lines of descent. One, determined by reduction in ovule-number coupled with aggregation of florets into dense inflorescences, leads to the Selagineæ of Bentham and Hooker. A second, determined by the adoption of a parasitic habit, leads to Orobanchaceæ, which are notable for the retention of what is probably a primitively unseptate ovary; the latter character seems to link this family with Gesneraceæ (*q. v. infra*). Another line, tending to *secondary* unilocularity of the ovary, leads to the highly-evolved Lentibulariaceæ, in which the ordinarily highest limit of economy in the andrœcium—invariably of two stamens only—is reached. The corolla, moreover, is usually highly specialized, as is also the habit.

These suggested evolutionary lines, together with the others with which we shall deal in the present chapter, are indicated in the accompanying diagram.

Two further lines of descent from the scrophulariaceous off-shoot of the Multiovulatæ-stock remain to be considered ; first, the line leading to Gesneraceæ, and thence, possibly, to Columelli-aceæ ; and second, the line terminated by Acanthaceæ.

MULTIOVULATAE	DIOVULATAE

ACANTHACEAE
III

LABIATAE

LENTIBULARIACEAE
I

Columelliaceae

GESNERACEAE
II

Orobanchaceae

Globulariaceae

I
SCROPHULARIACEAE
1

Pedaliaceae

Martyniaceae

BIGNONIACEAE
2

Phrymaceae

Myoporaceae

VERBENACEAE

MULTIOVULATE STOCK

DIOVULATE STOCK

(PLANTAGINALES)

TRANSITIONAL GROUP OF TUBIFLORAE

APOCYNAL STOCK
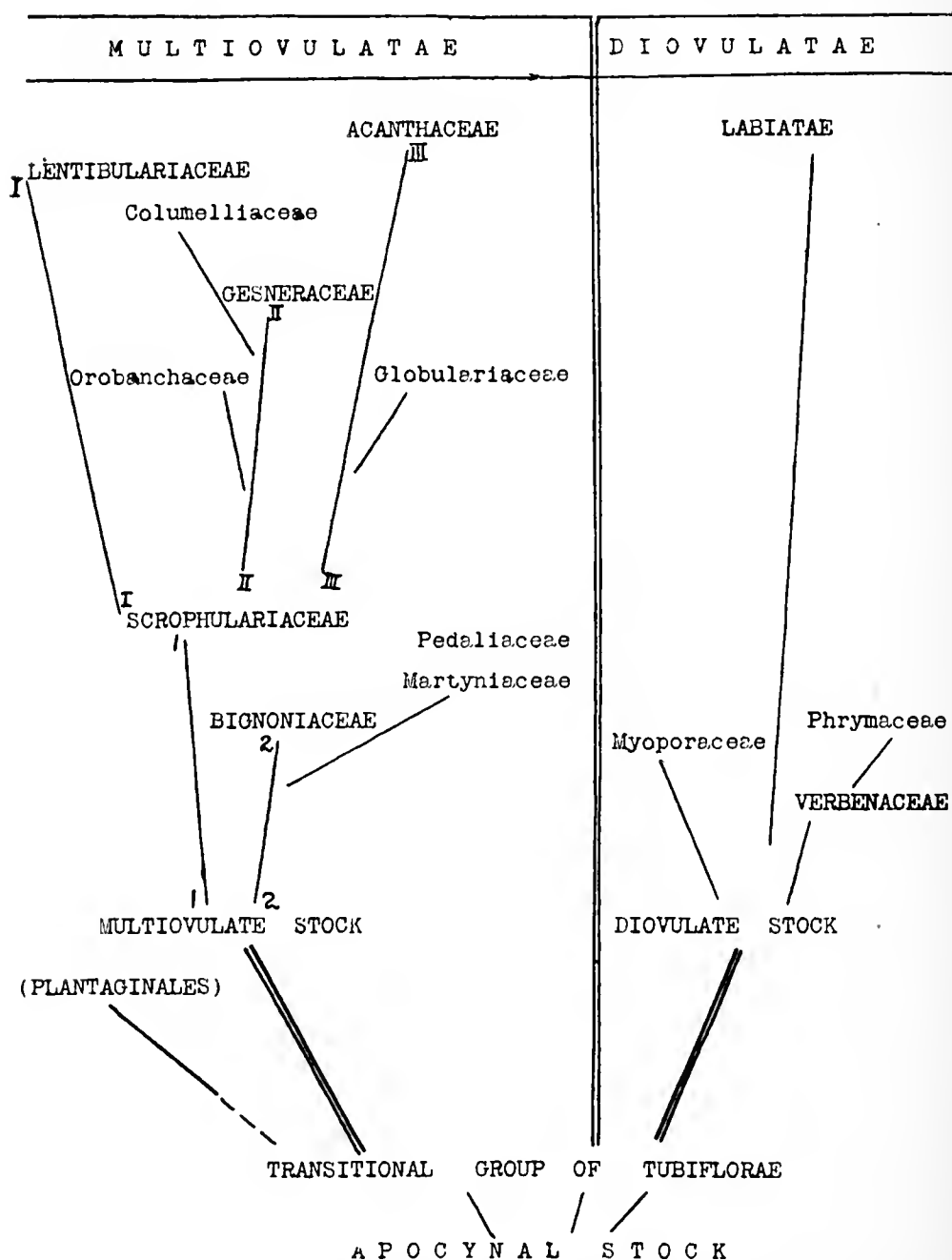
Diagram illustrating the possible affinities of the Higher Tubifloræ.

The Gesneraceæ are, with the rarest exceptions, herbaceous or suffruticose in habit. Considered from the point of view of advance upon the scrophulariaceous stock, the only material feature seems to be the enlargement or conspicuous colouring (often

	Engler.	Bentham and Hooker.	Approx. No. of Species.	Symmetry of Corolla.	Economy Tendency.				Special Adaptations to Insect Visits.	Fruit Character and Provision for Efficient Seed Dispersal.
					No. of fertile stamens (< C except where otherwise shown).	No. of Carpels.	No. of Loculi.	No. of Ovules per Loculus.		
SUB-COHORT C	SCROPHULARIACEÆ	SCROPHULARINEÆ	2000	Usually zygomorphic, sometimes sub-regular.	4 didynamous, 2 not rarely, 5=C in some cases	2, very rarely 3	... 2 ...	∞, with rare exceptions	Various (see text)	Capsule
SUB-COHORT C	LENTIBULARIACEÆ	LENTIBULARIEÆ	250	Strongly zygomorphic.	... 2 ...	... 2 ...	1, with free cent. placenta	∞		Capsule
SUB-COHORT C	OROBANCHACEÆ	OROBANCHACEÆ	125		4 didynamous	2, abnormally 3	1, with parietal placenta	∞		
SUB-COHORT C	GESNERACEÆ	GESNERACEÆ	700	Nearly always zygomorphic, rarely sub-regular.	4 didynamous usually, sometimes 2, rarely 5=C	... 2 ...	... 1 ...	∞	Enlargement of individual flower and conspicuous coloring	Capsule or Berry
SUB-COHORT C	COLUMELLIACEÆ	COLUMELLIACEÆ	2	Sub-regular or slightly zygomorphic.	... 2 ...	... 2 ...	1, or 2 by union of placentæ	∞		Capsule
SUB-COHORT C	BIGNONIACEÆ	BIGNONIACEÆ	500	Usually only slightly irregular.	4 didynamous usually, 2 very rarely, 5=C very rarely.	... 2 ...	2 usually, 1 sometimes	∞	Enlargement of individual flower	Capsule; winged seeds
SUB-COHORT C	PEDALIACEÆ	PEDALINEÆ	45	Not very strongly zygomorphic.	4 didynamous usually	... 2 ...	2 or more by secondary septa.	∞—1		Hooked woody fruits
SUB-COHORT C	MARTYNIACEÆ	PEDALINEÆ	6	Not very strongly zygomorphic.	4 didynamous usually	... 2 ...	... 1 ...	∞—few		Hooked woody fruits
SUB-COHORT C	GLOBULARIACEÆ	(in Selagineæ)	20	Markedly zygomorphic.	4 didynamous	2 (see text)	... 1 ...	1, pend. anat.	Aggregation into capitate inflorescences	Nutlets, dehiscent or not
D	ACANTHACEÆ	ACANTHACEÆ	1600	Zygomorphic; a good many sub-regular.	4 didynamous or 2, sometimes both in same genus	... 2 ...	... 2 ...	2 in most cases; 3 to 8 not rarely; seldom >8	Dense spikes; conspicuous bracts	Capsule opening elastically; seeds usually borne on hooked process
E	MYOPORACEÆ	MYOPORINEÆ	86	Usually irregular; sometimes sub-regular.	4 didynamous, rarely =C	2 usually	2 usually; occasionally 3—10	... 1—8 ...		Drupe
SUB-COHORT B	PHRYMACEÆ	VERBENACEÆ	1	Sub-regular in some; more commonly zygomorphic.	4 equal, or 4 didynamous usually; not rarely =C; sometimes 2	2; very rarely 4—5	4; very rarely 8—10	... 1 ...	Various (see text)	Drupe or berry
SUB-COHORT B	VERBENACEÆ	VERBENACEÆ	750	Sub-regular in some; more commonly zygomorphic.	4 equal, or 4 didynamous usually; not rarely =C; sometimes 2	2; very rarely 4—5	4; very rarely 8—10	... 1 ...	Various (see text)	Drupe or berry
SUB-COHORT B	(A Tribe of SCROPHULARIACEÆ)	SELAGINEÆ	About 120, incl'ded in Scrophulariaceæ	Sub-regular to strongly zygomorphic.	2 didynamous; 2 not rarely	... 2 ...	2—1 by abortion	... 1 ...	Aggregation into clusters and spikes	Two achenes, free at maturity
SUB-COHORT B	LABIATÆ	LABIATÆ	2800	Zygomorphic; occasionally sub-regular.	4 equal or 4 didynamous; often 2 only	... 2 ...	... 4 ...	... 1 ...	Aggregation into verticillasters and sometimes capitula	Schizocarp of four 1 seeded nucules
PLANTAGINALES	PLANTAGINACEÆ	PLANTAGINEÆ	200	Regular; tetramerous.	4 equal usually (see text) isomerous with corolla.	... 2 ...	usually 2; sometimes 3—4 by spurious septa; or in ♀ flr. 1	1—∞	...	Capsule, dehiscing with a lid.

(Bentham and Hooker column grouping: COHORT PERSONALES covers Scrophularineæ through Pedalineæ; COHORT LAMIALES covers Acanthaceæ through Labiatæ; Anomalous Order covers Plantagineæ.)
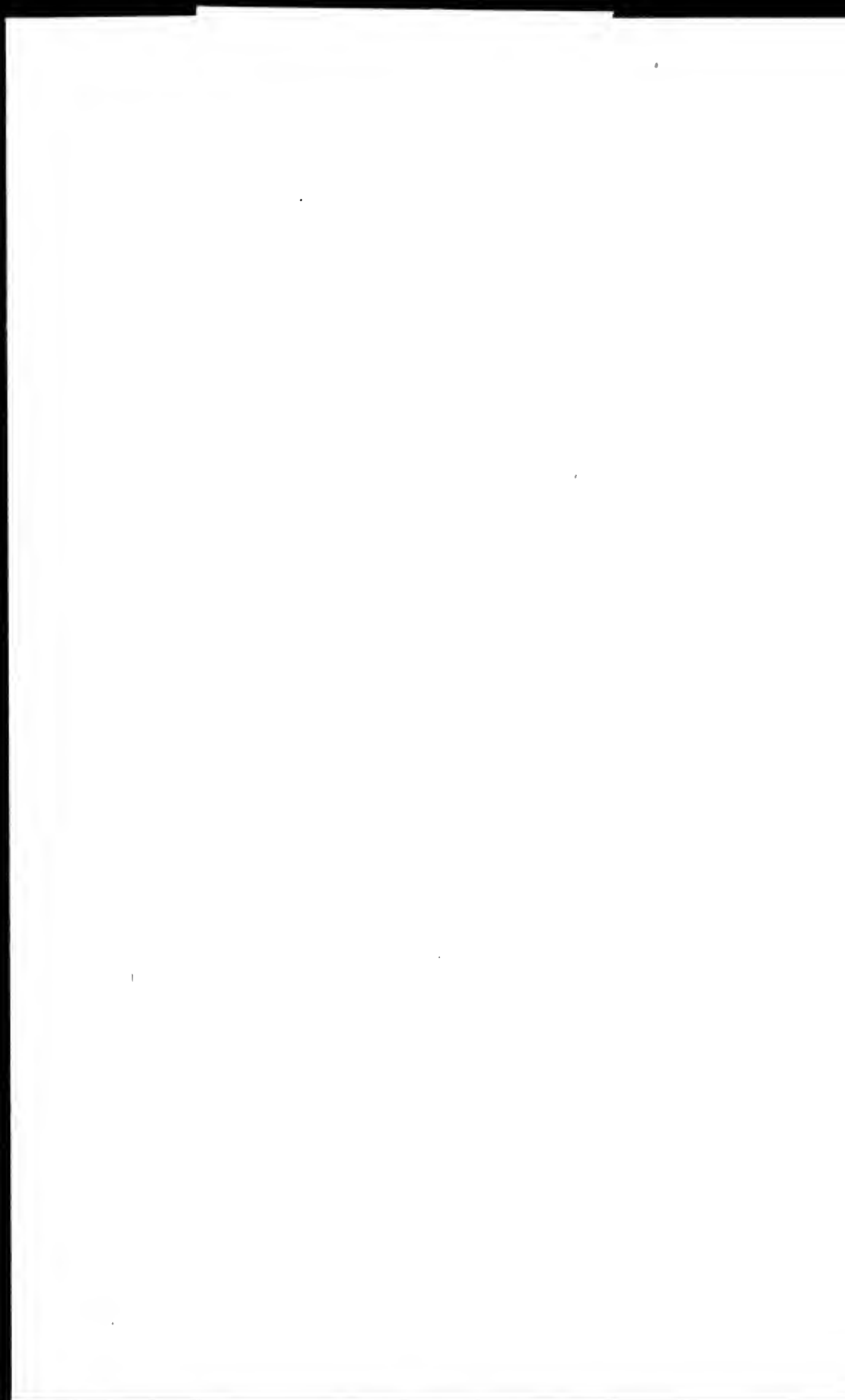
both) of the corolla; many of the Gesneraceæ have very brightly-coloured flowers, which in some cases attain a considerable size. They are, again, more or less specialized in habit, with a distinctive external *facies*—comparable with the similar condition which characterizes certain other families, such as Ericaceæ, Gentianaceæ, Labiatæ, etc.

In regard to economy of megasporangia, the Gesneraceæ are by no means advanced; the ovules are invariably numerous. The stamens are typically four in number, often with the staminodial remnant of a fifth; an andrœcium of two stamens is the exception. The stamens are arranged didynamously, and the members of a pair tend to approximate, and in some cases actually fuse; the possible significance of this will be referred to later. Relics of the ancestral regular flower with isomerous andrœcium are to be found, as in the case of *Verbascum* in Scrophulariaceæ. These relics include the genera *Ramondia*, *Championia*, *Conandron* and a few species of *Niphæa* and *Bellonia*—about a dozen species in all. Other relatively primitive features occur in Gesneraceæ, not merely exceptionally, but typically. The corolla is rarely, if ever, very highly specialized in shape or structure; it is usually tubular, with a more or less open mouth. The ovary, moreover, is unilocular, in the sense which we have described as primitive; and the fruit is not often very specialized. In the characters of the corolla, andrœcium and gynæcium, the Gesneraceæ resemble Orobanchaceæ very closely, and the latter family might reasonably be merged with the former.

The unilocular ovary is one of the chief distinguishing features of Gesneraceæ, and is practically without exception. The parietal placentæ in the several genera display all degrees of protrusion towards the centre of the ovary-chamber; but in no case do they actually meet and so form a septum except in *Monophyllæa* and *Loxophyllum*, comprising barely five species altogether. This mode of septation of the ovary has been referred to already; and its progressive action as an evolutionary tendency is recognizable in two large familes of the higher Tubifloræ, namely, in Gesneraceæ, where the septation is barely realized, and, as we shall shall see, in Bignoniaceæ, where a bilocular ovary is the rule.

The Orobanchaceæ and Gesneraceæ, then, represent the terminal points of relatively short and approximated lines emanating from the scrophulariaceous stock.

Before we leave the latter family we must refer to a striking tendency which distinguishes Gesneraceæ sharply from all other

families of Bicarpellatæ,—a tendency to epigyny. This is indicated in many and varied degrees of completeness, and more than 35% of the total number of species in the family are concerned ; these belong to the sub-family Gesneroideæ.   The existence of these degrees, varying from slight to almost complete epigyny, suggests rather strongly that the latter condition represents a tendency peculiar to Gesneraceæ—a *secondary* tendency towards epigyny, not comparable with the general (" calycifloral ") tendency to which attention has been drawn in our earlier chapters; in other words, Gesneraceæ have availed themselves, so to express it, of the advantages associated with epigyny, coupling it with characters typical of a highly-evolved member of the Bicarpellatæ plexus.   This conclusion seems to derive some support from the conspicuous absence of any such tendency from any other groups of the plexus,—and, indeed, from the remoter archichlamydeous stock to which this plexus is held to owe its origin.

How far this line of reasoning may be adopted in the case of other groups which differ essentially from their near allies only in the relative position of the ovary must be judged on the merits of each individual example.   The Vaccinioideæ provide a case more or less in point (chapter III) ; they will be examined from this aspect when we come to deal with the large groups of Sympetalæ characterised by epigyny.

The epigyny-line seen in Gesneraceæ is realized in the small family Columelliaceæ, consisting of two or three species only, shrubs of western tropical America.   The corolla is sub-regular, of the *Ramondia* type, with a short tube.   The andrœcium consists of two stamens constantly, but there is reason to suppose that each is the fusion-product of a pair of stamens ; in any case the resemblance to Gesneraceæ is clear.   Further, the inferior ovary shows transition from the unilocular to the bilocular state, the latter resulting from the union of the projecting placentæ.   The ovules are numerous.   The systematic position of Columelliaceæ has been made matter for considerable doubt, and they have been variously placed in different systems ; the two modern systems agree in associating them with Gesneraceæ.   They are an old family from the point of view of descent ; and this, coupled with their shrubby habit and their resemblance in so many essential points to Gesner-aceæ—especially to those with a corolla of relatively primitive type—favours the suggestion that they may be the sole surviors of that branch of the scrophulariaceous stock from which Gesneraceæ have been derived.

The suggestion has been advanced that this branch with its tendencies to epigyny and syngenesis of anthers may have given rise to the higher groups with inferior ovary, or at least to some portion of them ; but it must be remembered that the stock in question is essentially oligomerous in the andrœcium, while the " Inferæ " are isomerous.

We turn now to an extensive family of high specialization and complexity, the Acanthaceæ. Alone of the Multiovulatæ does this family at all approach Scrophulariaceæ in point of number of species, comprising as it does rather more than three-fourths of the number of species in the latter. The Acanthaceæ are mostly shrubby or suffruticose ; some are herbaceous, but trees are rare. They are extremely common in tropical regions, where they constitute the greater part of the weedy vegetation ; very few are extra-tropical.

The distinctive characters of the family are concerned with conspicuousness of both the individual flower and the inflorescence, with anther-specialization, and with seed-distribution. The inflorescence, often spicate, is typically associated with conspicuous and often highly-coloured bracts. The flowers are, relatively speaking, generally large—as compared, for instance, with those of Scrophulariaceæ. The corolla is frequently strongly zygomorphic, often elaborately bilabiate ; at the same time sub-regular corollas with lobes almost equal are by no means uncommon, especially in those forms which are in other respects relatively primitive.

The andrœcium displays marked advance. It is anisostemonous almost without exception (*Pentstemonacanthus*). In about 40% of the species, the stamens number four ; in 15%, four or two ; while in about 45% the andrœcium consists constantly of two stamens only. In the more advanced forms (*e.g.*, Justicieæ) the anthers are variously modified, doubtless in relation to pollination, although the details are practically unknown in most cases. A common form of modification consists in the inequality and sterilization of one of the anther-cells, which may become elaborated in various ways.

Staminodes are of common occurrence, especially in the flowers with only two stamens ; in the tetrandrous flowers, however, the posterior stamen is rarely represented in any form. According to Payer, five primordia are invariably present in the young andrœcium of *Acanthus mollis*, but the posterior one aborts at a very early stage.

It is in the ovary and fruit that Acanthaceæ are most notably advanced. There is a strong tendency to reduction in ovule-number, and this, we shall see, in probable relation to seed-dispersal; this reduction proceeds more or less hand-in-hand with reduction in the number of stamens. The bicarpellary ovary, which is almost always bilocular, rarely contains more than eight ovules in each loculus; and in any case the ovules are never very numerous. In the tribe Nelsonieæ the number is indefinite, and the ovules are arranged in two series. In Ruellieæ the number is more or less indefinite, but rarely exceeds eight; and there are most commonly four stamens with anthers equally bilocular. In the higher members of the family, comprising about three-fourths of the total number, there are regularly two ovules to each carpel. This latter character will be readily distinguished in its significance from the exactly similar condition which obtains in the Diovulatæ. In the latter case the condition is practically fixed, and already laid down in the ancestry; in the present case the diovulate forms are closely con-nected with multiovulate species within the limits of the same family. This series of forms reflects a special tendency which has seed-dispersal as its ultimate aim. The fruit is nearly always capsular, rarely baccate (*Mendoncia*). The capsule is usually short, and is loculicidal right to the base; on the strength of this character Engler has separated Acanthaceæ as a sub-cohort distinct from C (see table, p. 152), in which the dehiscence-line barely reaches the base of the fruit. The latter usually bursts elastically with some violence; and the ejection of the seeds is aided by rigid hooked processes (*retinacula*), which may be outgrowths either of the funicles or of the placentæ. The reduction in ovule-number is without doubt correlated with the appearance of these woody processes, as will be readily conceived, seeing that each seed is associated with a retinaculum; and the seeds, in correspondence with their diminished number, are relatively large, and they are often compressed. It need scarcely be pointed out that a few large flat seeds may be thrown from a bursting capsule to a greater distance than many small rounded ones.

In view of the several complexities described in the foregoing, we are led to regard the Acanthaceæ as representing the most highly-evolved among the living descendants of the multiovulate stock. In a type illustrating the upper limits of advance along the different lines indicated above, the large flowers will be borne in a more or less condensed inflorescence with conspicuous bracts, the

corolla will be strongly zygomorphic and of elaborate structure; the stamens will number two only, with no trace of staminodes; each anther will possess but one fertile pollen-sac, the other being modified for purposes of attraction, pollination-mechanism, etc.; the bilocular ovary will contain two ovules in each loculus; and the two-valved, explosive capsule will contain four large compressed seeds, each carried upon a woody, hooked process. Forms embodying most of these characters are common among the higher Acanthaceæ (e.g. Justicieæ).

The Acanthaceæ represent the terminal point of their branch of the evolutionary tree; we have now to consider their points of contact with less advanced groups. The Transitional Group is recalled in the Thunbergieæ, in which many characters of an ancestry which produced Convolvulaceæ are preserved. The members of this section, unlike the rest of the family, are mostly twining plants, and include about 100 species. The flowers are typically large, with sub-regular corollas contorted in æstivation; the ovary contains two ovules in each of its two loculi. In *Mendoncia*, with twenty-five to thirty species, the fruit is a berry and there are no retinacula; and in *Thunbergia*, with a capsular fruit, the retinacula are represented by cupular structures which are funicular in position and apparent origin, becoming horny at maturity. The resemblance between this section and Convolvulaceæ is remarkably strong, both superficially and in detail. But the anisostemonous andrœcium (four stamens) and the primitive retinacula of *Thun-bergia* justify its inclusion in the higher family.

A second small section, *Nelsonieæ*, represents the link with Scrophulariaceæ; the ovules are indefinite and the retinacula represented by small papillæ. A third section, Ruellieæ, may be regarded as a final transition to the higher Acanthaceæ; here the ovules are indefinite but few, with typical retinacula; the stamens usually number four, and the anthers are rarely modified to any extent.

The families with which we have dealt so far have all been regarded as offshoots from the scrophulariaceous stock. We now come to deal with a group which seems to approximate more closely to the remoter Multiovulatæ-stock (see diagram, p. 152) in so far as it retains unmistakeable traces of the characters of the apocynal plexus (see chapter V). The chief family concerned is Bignoniaceæ. These, unlike any family of Multiovulatæ so far considered, are usually trees or shrubs, very often climbing plants, very rarely

herbaceous (*Argylia, Incarvillea*). They inhabit the tropics, chiefly those of South America, where they are said to form a conspicuous feature of the liane vegetation. They are further exceptional among sympetalous woody plants in the frequent possession of compound leaves. We have already drawn attention to the relative rarity of this character among sympetalous trees, while it is quite common among polypetalous woody plants—*e.g.*, Leguminosæ, Sapindaceæ, Rutaceæ, Meliaceæ, etc. We are thus led to surmise that the Bignoniaceæ may be, relatively speaking, a primitive group, since its members share a conspicuous common character with Archichlamydeæ ; and this finds some support in the presence of a woody habit among members of these higher groups, whose main tendency is towards a herbaceous habit (see chapters IV, V).

Let us examine whether this surmise is justifiable; in other words, whether Bignoniaceæ stand near the apocynal-multiovulate stock. The climbing shrubby habit and opposite leaves certainly recall Apocynaceæ, and further links with that family are not wanting. The mode of seed-dispersal is essentially the same, provision being made for the individual dispersal of a large number of seeds from a dehiscent fruit (see last chapter); but in Bignoniaceæ the seeds are usually winged, not comose. At the same time winged seeds are not altogether rare in Apocynaceæ. The corolla in the former family is, in most cases, almost regular with a broadly open mouth ; irregularity rarely proceeds much further than a bending in the corolla-tube or the lateral facing of the flower and a slight obliquity of the corolla-limb.

It is especially the andrœcium which justifies the inclusion of Bignoniaceæ among the higher groups of Tubifloræ, for it is anisostemonous. The oligomery of the stamens has, however, not proceeded far ; for the flower has nearly always four stamens, with a fifth represented by a staminode. The latter is remarkably constant throughout the family, the sole exception, apparently, being the genus *Argylia*. Payer found that in the developing flower of *Bignonia grandiflora* five staminal primordia are laid down ; the posterior stamen never becomes fertile, but persists as a simple filamentous staminode.

In *Catalpa* (about six species in all) three members of the andrœcium are staminodial, only two being fertile stamens. The isomerous andrœcium, on the other hand, is equally rare, occurring in about seven species only (*Oroxylum, Rhigozum, Catophractes*).

The ovary is typically bilocular as in the parent apocynal

stock; but in *Eccremocarpus* and the tribe Crescentieæ (formerly separated as a distinct family) the ovary is unilocular and the placentation parietal. Septation is, however, foreshadowed in these forms, for the protruding placentæ sometimes meet, especially near the base of the ovary. These exceptions to the bilocular condition represent about 7% of the whole family. The Crescentieæ, moreover, differ from the rest of the family in their fruits, which are indehiscent, either fleshy or dry.

Enough has been said, perhaps, to favour the suggestion that Bignoniaceæ lie nearer to the ancestral stock than any other group of the Multiovulatæ. Indeed, it will be gathered that their advance upon that stock is little, if any, greater than the minimum required to justify their inclusion in the last-named group; their position is thus indicated on the diagram, p. 152.

An offshoot of the bignoniaceous line is represented by the families Pedaliaceæ and Martyniaceæ, included in one family, Pedalineæ, by Bentham and Hooker. Their affinity with Bignoniaceæ is evidenced by their sub-regular flowers and usually didynamous andrœcium, often with a posterior staminode; the latter is, however, small, and sometimes wanting. Their advance upon Bignoniaceæ is seen in their constantly herbaceous habit, and particularly in the fruit-character. The tough capsule-wall is produced into woody hooks, spines, etc., which may aid in the dispersal of the fruit by anchoring it in the wool or fur of animals. The ovary may be 1- or 2- locular at first, but there is a distinct tendency to chamber the developing fruit by the division and protrusion of the placentæ; this is coupled sometimes with a reduction in the number of ovules and seeds.

* * * *

This completes our examination of the Multiovulatæ, and our conclusions as to the general lines of affinity within the group are shewn in the diagram, p. 152. This includes also the Diovulatæ, and a vertical double line separates the two groups; those members of the Multiovulatæ in which the number of ovules is reduced appear correspondingly near to this dividing line. The latter is regarded as a more or less sharp one, and the two groups fall on either side of it as the respective products of two lines of descent diverging from the apocynal stock (see chapter V) and emerging already within the Transitional Group.

We now turn to the other branch :—

The Diovulatæ.

The essential characters of this group are included in the table on p. 152, and their affinities indicated in the diagram on p. 152. A striking feature in regard to this branch as compared with the Multiovulatæ is the small number of families—practically three only—into which it may be naturally divided; and of these over 75% fall into one very natural family, Labiatæ.

The key-note of the Diovulatæ, we have seen already, is schizo-carpy, the tendency to associate each seed with a separate fruit-covering. This tendency we have discovered in the Transitional Group, and we have observed it in a high degree of realization in Boraginaceæ.

Schizocarpy clearly involves reduction in the number of ovules; this is reflected in a leading character of Diovulatæ, namely, the presence of two ovules only to each carpel. This character is remarkably constant throughout the group, as is also the bicarpellary condition of the ovary, although in some cases the true primary structure is masked by the early initiation of secondary septation. The largest group, Labiatæ, is so well-defined for the most part, so constant in essential characters, and possessed of so characteristic a "facies," that we are led to a *primâ facie* presumption that it is relatively advanced; this, we shall find, is probably the case.

The remaining members of the Diovulatæ are comprised in the families Verbenaceæ (with Phrymaceæ) and Myoporaceæ.

We may premise that Verbenaceæ display many evidences of relative primitiveness. In the first place, many trees and shrubs are included in the family, and a good number with compound leaves (*Vitex*). In no small proportion (about 14%), again the corolla is nearly or quite regular with isomerous andrœcium (some Chloantheæ and Viticeæ). In nearly 80% of the family oligomery of the andrœcium has proceeded only so far as the abortion of one stamen of the ancestral pentamerous whorl,[1] leaving barely 8% with diandrous flowers—a somewhat striking contrast with the corres-ponding figures for Scrophulariaceæ, 30%, and Acanthaceæ, 50%. Even in Labiatæ, we shall find, diandrous flowers occur in less than 25% of the species, so that in this regard the Diovulatæ as a whole are not nearly so far advanced as the Multiovulatæ.

[1] Curiously enough, however, all trace of the ancestral posterior stamen has been lost in the ontogeny of those forms examined by Payer (*loc. cit.* p. 559). He finds that only four staminal primordia are laid down in the case of *Lippia citriodora, L. repens, L. chamædrifolia, Verbena pulchella,* and *Spielmannia africana*; a pair of anterior stamens appear first, then two lateral members.

What we must regard as a further and important primitive feature in Verbenaceæ is the relatively low degree which the schizo-carpic tendency has attained in this family. The ovary is usually almost entire in external form, although its internal chambering into uniovulate compartments is active and unmistakeable. The result in the fruit is a chambered drupe; and this condition may be regarded as a primitive step towards the true schizocarpy characteristic of Labiatæ. Each seed is protected independently, but cannot be dispersed independently from the outset. The same transition is observable in Boraginaceæ, as witness the distinction between the drupaceous fruits of Cordioideæ, Ehretioideæ and Heliotropioideæ, and the schizocarps of Boraginoideæ.

In view of the foregoing, we are led to place Verbenaceæ relatively low in the evolutionary tree (see diagram, p. 152), in a position corresponding with that assigned to Bignoniaceæ in the case of Multiovulatæ.

In regard to the special lines of evolutionary advance within the family, these are the reverse of distinct. In habit the Verbe-naceæ display considerable diversity, as is to be expected in view of their relative primitiveness. They may be trees, shrubs, or herbs; lianes occur fairly commonly; but no general distinctive facies is peculiar to the family as a whole. Perhaps the most definite tendency is towards the close aggregation of florets, resulting in the common occurrence of spikes and heads, often associated with involucres of coloured bracts. The flowers are sometimes very large, in some cases with very long corolla-tubes (*Clerodendron*).

The aggregation-tendency is particularly noticeable in the herbaceous forms, and we shall find it reflected as a common character in Labiatæ. Before we deal with this family, we must refer briefly to the other two families which appear in Engler's group B of Tubifloræ.

Phrymaceæ, containing a single species only, *Phryma lepto-stachya*, is included in Verbenaceæ by Bentham and Hooker, but separated as a distinct family by Engler on the ground that the erect ovule is orthotropous, there being no transitional stages to this condition in Verbenaceæ. The ovary is unilocular and uni-ovulate. The plant in question is herbaceous, with the habit and facies of *Priva*, a truly verbenaceous genus. It would be out of place to discuss in detail here the systematic position of *Phryma*, but it may be suggested that the ovary may represent the remnant of an ancestral group of nucules, the rest having aborted—a process

similar to that by which Globulariaceæ descended from Selagineæ (*supra*).   Evidence of arrested development of loculi is not wanting among Verbenaceæ, and the nucules in the fruit of some Labiatæ may number three, two, or one only, owing to abortion.

Apart from the characters of the gynæcium, *Phryma* is undoubtedly verbenaceous.

Myoporaceæ includes less than 100 species, chiefly Australian and Polynesian.   Their usually anisostemonous andrœcium with didynamous stamens and more or less irregular flowers entitle them to a place among the higher Tubiflorae ; but their exact position within the latter group has been regarded as questionable.   Eichler and Bentham and Hooker associate them with Diovulatæ ; Engler assigns them the rank of a separate sub-cohort of Tubiflorae, placing them after his multiovulate groups and widely removed from sub-cohort B (Diovulatæ).   The question turns principally upon the number and arrangement of the carpels, seed-chambers, and ovules. It is probable that in all cases the ovary is primarily bicarpellary ; and in all the genera except *Myoporum*—i.e., in nearly three-fourths of the total number of species—the ovary is constantly bilocular. In *Myoporum* (20 species) the number of loculi is indefinite (2 to 10), and this is due to secondary septation ; the motive of the latter is reflected in the fact that only one ovule is present in each chamber of the multilocular forms, while in the bilocular forms more than one may be found.   In *Eremophila*, the largest genus (40 species), there may be four, six or eight ovules in each of the two loculi, superposed in pairs ; there are rarely so few as two. *Pholidium*, with 15 species, is entirely typical of Diovulatæ in having two ovules (rarely one) associated with each carpel.

The occurrence of indefiniteness in ovule-number may be regarded as favourable to the inclusion of Myoporaceæ in Multi-ovulatæ ; but the clear tendency to schizocarpy by secondary segmentation is still more favourable to their classification with Diovulatæ.   The position of Myoporaceæ relatively to Diovulatæ will then be seen to be comparable with that of Nolanaceæ relatively to Boraginaceæ, in the Transitional Group (see chapter V) ; for in either case the ovule-number is indefinite in the questionable group, but the latter is linked with the family having definite ovule-number by the character of schizocarpy.

Other considerations support the suggested affinity of Myo-poraceæ with Diovulatæ.   They recall the verbenaceous *Avicennia* closely in general habit, and the drupaceous fruit is practically

identical with that typical of Verbenaceæ. Fruits of this type do not occur in Multiovulatæ; and seeing that the schizocarpic tendency is here regarded as a fundamental principle of distinction between Multiovulatæ and Diovulatæ, we must regard Myoporaceæ as a member of the latter group. They may thus represent the earlier progeny of the Diovulatæ-stock, prior to the establishment of a fixed and definite number of parts in the fruit.

There remains for consideration the largest and most advanced family of Diovulatæ, Labiatæ. This family is of world-wide distribution, in contrast to Verbenaceæ, most of which are confined to tropical or sub-tropical regions; and with very few exceptions these are herbaceous. The ovary is typically four-celled and four-lobed, the latter more or less deeply; the resulting fruit is the familiar schizocarp of separate one-seeded nucules. It is chiefly in the character of the ovary and fruit that Labiatæ differ from Verbenaceæ critically; but their distinction from the aspect of special evolutionary advance is marked enough. The lines of advance upon the ancestral stock typified in Verbenaceæ find expression first, in the establishment of the herbaceous habit with its very characteristic external features—square stems, decussate or whorled leaves, aromatic odour, etc.; and second, in the aggregation of the flowers into dense inflorescences. The latter condition, foreshadowed already in Verbenaceæ, is the rule rather than the exception in Labiatæ, and is illustrated in the common but peculiarly labiate type of cymose cluster known as the *verticillaster*. Close, involucrate capitula are not uncommon.

The corolla ranges from sub-regular to strongly and elaborately zygomorphic, and from very small and inconspicuous to fairly large and brightly-coloured types. But conspicuousness is, of course, attained fundamentally by aggregation (*supra*). The andrœcium is usually tetrandous and didynamous; in 22%, only, are the flowers diandrous. Staminodes are not common, and are small when present. Payer (*loc. cit.* pp. 553–557) records his investigation of the floral development in *Stachys recta, Lavandula densa, Perilla arguta, Salvia patens.* In all these cases five staminal primordia appear, successively, in an anterior to posterior direction. In *Stachys* the posterior stamen aborts almost as soon as it appears; in *Lavandula* it persists for a time. In the diandrous *Salvia* the laterals abort as well, and only the two highly-complicated anterior stamens remain.

The Labiatæ are clearly a very natural group and represent the highest terminal point of evolutionary progress for the Diovulatæ,

standing to that group in much the same relation as Acanthaceæ
to Multiovulatæ; in both cases the chief principle underlying advance
has been efficient seed-dispersal, but each has acquired efficiency
in a distinct way.

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With a brief summary we may now dismiss the Tubifloræ.
This large cohort, in spite of the numerous families which it includes,
is a remarkably natural group, in so far as these families can be
combined into a single evolutionary tree in the manner we have
endeavoured to portray. At the root of this tree lies the apocynal
ancestry, characterised by regular flowers and isomerous andrœcium.
These characters are retained in those families which first emerged,
the Transitional Group ; in the latter the chief tendency is towards
fruit-specialization, as expressed in schizocarpy. This tendency led
to the differentiation of two main branches, each determined by
zygomorphy, but mutually distinguishable on the ground of schizo-
carpy with its attendant tendency to reduction in ovule number.

This distinction is already well established in the Transitional
Group, as witness the schizocarpic Nolanaceæ and Boraginaceæ as
compared with the non-schizocarpic Hydrophyllaceæ and Solanaceæ.
Convolvulaceæ are regarded as terminating the short main trunk of
the tree before us (see diagram, chapter V), while Polemoniaceæ
represent a branch arising adventitiously, so to express it, from
the roots.

The two branches in question give rise to the respective
stocks of Multiovulatæ and Diovulatæ. The subsequent branches of
the latter are but few (see diagram in present chapter), the fruit-
character being already well-defined. From the former two stocks
emerge ; one, a short one, produces Bignoniaceæ, and, by further
elaboration of the fruit, Pedaliaceæ and Martyniaceæ ; and the
other becomes the stock of Scrophulariaceæ, with relatively
unspecialized fruit. From the last-named stock three ultimate
branches arise, leading, 1st, to Lentibulariaceæ, with extreme
specialization in structure and habit ; 2nd, to Gesneraceæ with its
allies Orobanchaceæ on the one hand and Columelliaceæ on the
other, the main feature of this branch being the tendency to
epigyny ; and last, to Acanthaccæ with highly complex mechanism
for seed dispersal, Globulariaceæ representing an early-emergent
side-shoot of the same branch.

Two broad principles govern the branching of the tree which
we have described, namely, the advantage of an efficient means for

seed-dispersal, and the advantage (previously described) of the herbaceous habit.

   *   *   *   *

It will be well to introduce at this point a group which is admittedly isolated :—

PLANTAGINALES.

The problematical nature of the affinities of this group is expressed in the systems of both Engler and Bentham and Hooker. The latter name it an " anomalous order," without attempting to find a place for it in their scheme ; Engler ascribes cohortal rank to the group, Plantaginales following immediately upon Tubifloræ; Warming includes them in Personatæ, a group corresponding approximately to Multiovulatæ.

All save two or three species (*Littorella, Bougueria*) belong to the familiar genus *Plantago*, with about 200 species scattered over the world but occurring mostly in temperate regions, especially of the northern hemisphere. The plantains are remarkably constant in habit, particularly in regard to the inflorescence-character; the small flowers are almost invariably aggregated into dense spicate or capitulate inflorescences.

The main features of the floral structure are as follow :—The corolla is regular and tetramerous ; the stamens are equal in number to the corolla-segments and alternate with them ; the ovary is usually bicarpellary and bilocular, with one or more ovules in each loculus ; the fruit is usually a capsule with transverse dehiscence.

Various and diverse suggestions have been made in regard to the affinities of Plantaginaceæ. The view most in favour at the present time seems to be that they represent the reduced progeny of an ancestral stock in Tubifloræ. That they represent a group reduced in descent seems undoubted, if only for the reason that, in spite of the advanced character of the inflorescence in relation to insect-visits, they are usually wind-pollinated,—as witness their long exserted filaments, versatile anthers, powdery pollen, etc.

The tetramerous flowers have been compared with those of *Veronica*, emphasis being placed upon the fact that the calyx-segments in both are placed diagonally with relation to the floral axis.[1] Significance has been laid on the superficial resemblance between the spicate inflorescences of some species of *Veronica* and

[1] Eichler, *Blüthendiagramme*, I, pp. 209, 210, 225.

those common among plantains. The diagonal placing of the calyx-segments has led to the assumption that a posterior calyx-segment has been lost in *Veronica* and *Plantago* in the course of descent. But in the allied *Littorella* the calyx-segments are not arranged diagonally (see Eichler, *Blüthendiagramme*, I, fig. 27). It has been assumed further that the tetramerous condition in both has resulted from fusion of two corolla-lobes. This may not impossibly be the case in *Veronica* with its unequal corolla-lobes and its affinities with pentamerous forms of the same family; but to make the same assumption in the case of *Plantago* with its perfectly regular corolla seems to be quite unwarranted. In neither *Veronica* nor *Plantago* do the processes of floral development favour the assumptions in question, in regard to either calyx or corolla.[1]

The androecium of *Plantago* is thus in every sense isomerous with the corolla, and this militates further against the idea of its origin from a stock which is essentially anisostemonous.

We conclude, therefore, that the ancestry of Plantaginales must be sought more remotely than among the descendants of Multiovulatæ, and we are led to regard them as derived from the apocynal plexus on an evolutionary branch contemporary with the branches of the Transitional Group; the original tendency determining the branch was aggregation of florets; but reduction supervened, the result, perhaps, of the adoption of a geophilous habit.

[1] Payer, *loc. cit.*, pp. 543, 607.

ON THE RELATION OF *LINARIA ALPINA* TYPE TO ITS VARIETIES *CONCOLOR* AND *ROSEA.*

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THE type form of *Linaria alpina* is distinguished from the varieties *concolor* and *rosea* by differences in the colouring of the corolla. In the type form the corolla is deep blue except on the ridges of the palate where it is orange or orange-yellow. Just within the throat, and concealed by the upper lip, there is also a double line of orange due to the presence of orange-coloured hairs on either side of the channel leading down to the opening of the spur. The orange colouration is mainly due to the presence in the papilliform epidermal cells of the palate and in the long hairs of the beard of a viscous orange-yellow fluid which does not immediately diffuse out of the cells when they are ruptured. But there is also a certain amount of colour in the cuticle, the numerous projections which cover the whole surface of the exposed cell-walls being distinctly yellowish.

In the variety *concolor* the orange colour is absent from the palate, the ridges either showing white or becoming so invaded by the surrounding blue that the flower appears self-coloured: the hairs in the throat however are coloured as in the type.[1] Coloration of beard and palate are evidently distinct characters. In this form then we have not absolute inability to produce a certain coloured substance which is found in the type, but only inability to form it in a particular region.

In the variety *rosea* beard and palate are coloured as in the type, but the colour of the rest of the flower is pink instead of blue. Here the blue colouring matter is not formed at all.

As regards distribution, the type form and *concolor* are both common in some localities, occurring often within a few yards of one another; in other places one form only may be found, or one may be far more abundant than the other. Thus according to Knuth[2]

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[1] In neither form as a rule is the beard visible unless the lips are pressed apart, but occasionally a few hairs may be seen protruding in unhandled flowers. In the type form this condition may easily escape notice, since the orange of the beard then appears merely as a continuation of the orange of the palate, but in the *concolor* variety a spot of orange in an otherwise wholly blue flower is noticed at once. This, it must be noted, is quite a distinct feature from the palate character.

[2] Handbook of Flower Pollination, Vol. 3, p. 176.

the type is the more common form in the Alps, the variety in the Pyrenees, the variety being chiefly found on granite in Switzerland according to Schinz and Keller.[1] In Tirol, Vorarlberg and Liechtenstein, on the other hand, Dalla Torre and Sarnthein[2] state that the *concolor* form is almost more frequent than the type Certain stations are also mentioned by these latter authors when *rosea*—a much rarer form—has been observed to occur wild.

Cross-breeding experiments were begun in 1898 and repeated in 1899, but the small number of germinations obtained and pressure of other work led to the abandonment of the experiments for the time being.   More recently the experiments have again been repeated, and as the later results are in agreement with those obtained earlier, we may regard them as sufficiently conclusive, although the total number of plants raised is small.   The number of germinations in each case was disappointingly few, but whether owing to failure to achieve the right conditions, or to the fact that much of the seed was not really good, it is difficult to say.   Another circumstance also tended to limit the number of plants raised.   It was found that an individual, if covered, or if isolated uncovered, generally failed to set seed;   hence, in order to obtain the F_2 generation without artificial fertilisation, it was necessary to place the F_1 plants at least two together under conditions in which they might be visited by visits without risk of being crossed with the parent forms.

Results of Experiments.

Three forms were employed, *viz :*—

1, *alpina* type ; corolla blue with orange palate.

2, var. *rosea* ; corolla pink   „   „   „

3, var. *concolor* ; corolla blue, orange absent from the palate which may be whitish or more or less deeply overspread with blue.

A few crossbreds were raised in 1899 and 1900 from reciprocal matings between the type and *concolor*, and later others were obtained from matings between *concolor* and both the forms with orange palate.   *All the F_1 plants resembled* concolor, *the orange colour being absent from the palate.*   In some flowers the corresponding or a somewhat smaller area of the under lip was whitish in colour, in others on the same individual the whole palate might be

[1] Flora der Schweiz, 1900, p. 453.

[2] Die Farn- und Blüthenpflanzen von Tirol, Vorarlberg und Liechtenstein III, p. 250.

suffused with blue so that the flowers appeared entirely self-coloured.[1] In the F_2 generation obtained by allowing the F_1 plants to inter-breed, the numbers indicated the simple Mendelian ratio of three without orange to one with orange on the palate.[2] In a case where a *concolor* plant supposed to be pure, but which proved to be a crossbred, was crossed back with the type, the offspring were mixed in approximately equal numbers.

These results show that in Linaria alpina *the pink colour of the variety* rosea *is recessive to the blue colour occurring in the type and in the variety* concolor; *and that, as regards palate character, presence of orange in the type and in var.* rosea *is recessive to its absence in var.* concolor. The dominance of blue over red shades is a relation with which we are now familiar in several genera, *e.g.,* Stocks, Sweet Peas, Salvia Horminum and others, and in the present case as in these other genera the effect is no doubt due to a factor which when present turns the red colour to blue. The dominance of the palate character, absence of orange, was somewhat unexpected in view of the fact that in another species—*L. vulgaris*, where the type form is distinguished by the presence of a similar orange-coloured area on the palate, and the variety *(perlutescens)* by its absence, the relation between the two has been found by de Vries[3] to be exactly the opposite. Crossing *L. vulgaris* (pale yellow with saffron-yellow to orange palate) with the variety *perlutescens* (palate as well as the rest of the flower pale yellow) de Vries obtained plants all having the deep yellow palate. A repetition of the experiments in a later year gave the same result. In the F_2 generation the proportion of the two forms was about 75% with deeply coloured palate to about 25% self-coloured. We thus have the somewhat unexpected result that in two species belonging to the same genus, each having a type form and a variety differing from the type apparently in precisely the same respect, *viz.,* absence of a particular colour from a corresponding region of the corolla, the presence of this colour behaves as recessive to its absence in the one case *(alpina),* and as dominant in the other *(vulgaris).*

[1] Except in such case as that mentioned above when the end of the line of the beard becomes visible and just shows a point of orange at the closed lips.

[2] Among the *concolor* plants of the F_2 generation one individual was found to have a single stem bearing flowers showing some orange on the palate while all the flowers on the many other branches were typically self-coloured. No other instance of what seems to have been a bud variation was observed in any of the other plants.

[3] Die Mutationstheorie II, 1, 1902, p. 152.

THE INTERNATIONAL PHYTOGEOGRAPHICAL EXCURSION IN THE BRITISH ISLES.

VII.—Pflanzengeographische Eindrücke auf den Britischen Inseln.

Von P. Graebner

(Gross-Lichterfelde, Berlin).

DER HAUPTEINDRUCK, den der aus Mitteleuropa in die einzelnen Teile der Britischen Inseln kommende Pflanzengeograph gewinnt, ist der, dass er in ein uralter Culturland kommt, in dem namentlich durch die ausgedehnte Viehzucht, in erster Linie durch die Schafe, die natürliche Vegetation auf dem grössten Teile der Fläche so verändert ist, dass es schwer ist, aus den jetzt dort vorhandenen Pflanzen sich ein Bild zu machen von den natürlichen Formationen, die dort geherrscht haben, bevor der Mensch das Land seiner Cultur unterwarf. Das typischste Beispiel welches uns auf der von Tansley so trefflich geleiteten Reise der Internationalen Phytogeographen deren floristiche Ergebnisse der Altmeister der Britischen Floristik, Claridge Druce, vor kurzem in gewohnter Sachkenntniss in diesem Blatte dargestellt hat, entgegentrat, war die Vegetation des Cross-Fell. Niemals sah ich irgendwo in Mitteleuropa Vegetationsformationen die derartig artenarm sind, wie verschiedene Flächen an den Abhängen und auf dem Gipfel eines solchen Berges. Natürlich ist daran nicht allein die Viehzucht Schuld, sondern die Eigenart des Klimas spielt eine grosse Rolle. Vergleicht man damit unsere doch im Wesentlichen unter gleichen Verhältnissen lebenden alpinen Weiden, so fällt den Unterschied besonders in die Augen. Auf einem Abhang gegen der Gipfel des Cross-Fell gelang es Dr. Rübel und mir z.B. trotz eifrigen Suehens keine andere grössere Pflanze zu finden als *Festuca ovina*, *Carex verna*, *Thymus serpyllum*, *Cerastium triviale*, *Cirsium lanceolatum*, *Galium Harcynicum* (*G. saxatile*) und dazwischen *Polytrichum*. Auf dem Gipfel wurde an einer grösseren Fläche in etwa 800m. in einem im Wesentlichen durch *Nardus stricta* und *Juncus squarrosus* gebildeten Bestande notiert: *Vaccinium myrtillus* (viel), *Cladonia rangiferina* (viel), *Potentilla silvestris* (*P. tormentilla*) und *Galium Harcynicum*. Nichts weiter!

Je schroffer die Felsen aufstreben, je mehr das Profil des

betreffenden Berges oder Abhanges steile Felsen zeigt, desto öfter finden sich Plätze an denen seltenere, an bestimmte physikalische verhältnisse gebundene Pflanzen vorkommen. Ben Lawers liegt allerdings in einer pflanzengeograpisch anderen Zone als Cross-Fell, die interessanten nordischen Elemente zeichnen ihn schon aus, aber auch wenn man die Zahl der verbreiteten Arten, besonders der Gebirgspflanzen, vegleicht, fällt ihre sehr viel grössere Zahl auf. Die Ursache möchte ich in dem Vorhandensein der in das Gestein eingesägten Rinnsale süchen, die für die Schafe etc. schwer resp. unbequem zugängliche Stellen schaffen, so dass ihre Vegetation nicht so oft von ihnen belästigt wird, resp. hier und da ganz unge-stört bleibt. Stellenweise finden sich auch hier ähnlich artenarme Flächen wie auf Cross-Fell, besonders die durch *Juncus squarrosus* hauptsächlich besiedelten Flächen bieten wenig Interesse, sehr viel mehr schon die schönen Weiden der *Alchimilla alpina* und je mehr man sich dem Gipfel nähert, desto mehr mehrt sich die Zahl der interessanten Gewächse; eine Perle ist die Einbruchstelle am Gipfel selbst, in die zum Teil in geringer Zahl sich einige Selten-heiten, die uns Professor Bayley Balfour in liebenswürdigste Weise zeigte, geflüchtet haben. Manche sonst seltene oder doch spärlich wachsende Arten werden dadurch, dass sie von den Vieh verschmäht werden, auffällig häufig, so z.B. *Lycopodium selago* und andere. Die characteristische " Schneethälchen "-Bildung der Alpen wurde von unseren Schweizerischen Reisegenossen mehrfach in schöner Ausbildung constatiert.

Der untere Teil der Berge war sicher früher bewaldet, namentlich die an den von uns besuchten Hügeln characteristiche dunkle Zone des Bestandes von *Pteridium aquilinum* war wohl die Region des Hochwaldes. Von unseren Mitteleuropäischen Halb-Culturformationen, einschliesslich der künstlichen Wälder etc., wissen wir, wie zähe die Waldpflanzen auch nach Vernichtung oder Umwandlung des Waldes sich oft erhalten. Auch die Englisch-Schottischen Berge geben davon Zeugniss; z.B. am Ben Lawers wächst an den schattigen Felsen viel *Luzula sylvatica* (*L. maxima*) mit anderen charakteristischen Bewohnern der Bergwälder.

Auch die Vegetation der Wälder, sowohl der Bestand des Waldes als die Beimischungen der Unterholzes und der Krautflora erscheinen en den meisten Teilen verändert. Auch hier ist in den meisten Fällen die directe Einwirkung der Viehzucht etc. sichtbar, dann aber auch Einbürgerung alter Culturpflanzen; so macht *Acer pseudoplatanus* so vollständig den Eindruck einer einheimischen Art,

dass man ihn ohne Kenntniss der Florengeschichte des Landes
dafür halten würde.

Unberührtes Hochmoor sahen wir in keinem Falle; alle zeigten
sie starke Veränderungen, meist Entwässerung und Verheidung;
unsere phytogeologischen Collegen werden die Veränderung der Flora
am besten constatieren können.   Sehr viele der oft dicken Moosmoore
trugen genau dasselbe Vegetationsbild wie ich es auf den sekundär
veränderten Mooren des nördlichen und besonders des nordwest-
deutschen Flachlandes zu sehen gewohnt bin.   Nirgend mehr sah ich
eine zusammenhängende *Sphagnum*-Decke.   An den ja auch in
Deutschland nur noch sehr spärlichen unberührten oder doch in
grösseren Teilen unberührten Mooren sind doch wenigstens an den
Senken und Rüllen solche *Sphagnum*-Flächen mit nur sehr zerstreut
eingemischter Vegetation phanerogamer Gewächse zu finden.   In
England überwiegen die letzteren fast überall.   Das oft massenhafte
Auftreten der Heidesträucher *Myrica gale* etc., ebenso wie der
Strauchformen der *Betula pubescens* und mancher Rasen oder
Bülten bildender Kräuter, wie z.B. der *Molinia cærulea* sind typische
Anzeichen der künstlichen Veränderung.   Auf eine solche möchte
ich auch das jetzige Aussehen der hochinteressanten und merk-
würdigen Moorformation zurückführen, wie sie sich im nördlichen
England findet, und wie sie uns in Gestalt des " Featherbed " und
" Hassock " unweit Huddersfield ein so interessanter Ausbildung
gezeigt wurde.   Von etwa ähnlichen auf der Höhe des Gebirges
gebildeten Hochmooren, wie wir sie in Mitteleuropa öfter z.B. auf
den " Brockenfeldern " im Harz finden, ist diese Formation durch
den fast gänzlichen Mangel an Strauchvegetation verschieden.
Eriophorum vaginatum ist vorwiegend; die Hänge, besonders die
nach N.W., sind oft mit dichten Bestände des *Rubus chamæmorus*
überzogen.   An den oben entwässerten Stellen tritt *Eriophorum*
oft zurück und an den trockneren Stellen findet sich *Calluna*, an
den feuchten *Juncus effusus*, also ein typisches Niederungselement,
an.   Unterhalb an den Hängen ist stellenweise viel *Betula* und
stellenweise kilometerweit *Pteridium aquilinum*.   Bei der grossen
hier herrschenden Niederschlagsmenge, *ca.* 125 cm. jährlich, müsste
hier eine ganz andere echte Hochmoorvegetation herrschen.
Anscheinend durch Nützung (Schaftrieb !) ist die für solche Flächen
in Mitteleuropa so charakteristische Strauchvegetation versch-
wunden oder doch zurückgedrängt.   Die Folge der damit ver-
bundenen Veränderung der Moosvegetation, etc. ist der geringe
Zusammenhalt der Mooroberfläche.   Bei starker Wasseraufnahme

des Moores wird die Gefahr des seitlichen Aufreissens, des Moor-
bruches, ständig vorliegen. Solche Risse in den Seiten des Moores,
die später natürlich ähnlich wirken wie künstliche Entwässerungs-
gräben, die dem Abfluss des überschüssigen Wassers dienen,
werden dadurch zu echten Erosionsfurchen, wie sie gerade die
genannten Moore der Hochfläche in grosser Zahl zeigten und wie
man sie (in sehr viel kleinerem Maasstabe) auch bei uns in
veränderten Gebirgsmooren findet. Dass auf die durch den
Moorbruch und die Erosion kahlgelegten Torfflächen in trocknen
Zeiten auch der Wind erheblich wirken muss, liegt auf der Hand.

Die Folge eines typischen Moorbruches sind meiner Meinung
nach die grossen Denudationsflächen die uns durch Dr. Lewis im
Kessel am Cross Fell gezeigt wurden. Die gesammte frühere
Vegetationsdecke dieses den Grund des Kessels früher füllenden
Moores war von seinen Rändern tief abgesunken. Das völlige
Zerreissen der ganzen Oberfläche in Stücke dürfte auch durch
Beweidung und der dadurch bewirkten geringen Haltbarkeit der
Pflanzendecke bewirkt sein. Es scheint als ob das Moor bei
Feuchtigkeitsperioden sich noch in Bewegung befindet.

Dass die Heide, besonders ihre hauptsächlichste Charackter-
pflanze *Calluna*, in dem feuchten Klima der Britischen Inseln in
Bezug auf ihre Standorte nicht wählerischer sein würde als bei uns
im Nordwesten, was vorauszusetzen. Thatsächlich trafen wir denn
auch mehrfach *Calluna* auf Kalk besonders im westlichen Irland,
z.B. bei Killarney, und besonders zahlreich und schön in Glenainagh
bei Ballyvaghan. Dort zählten Dr. Ostenfeld und ich über 100
Arten, eine bunte Pflanzengesellschaft. Allerdings waren auch hier
die durch den Weidebetrieb eingewanderten Arten nicht selten, aber
die Steilheit der Abhänge ermöglicht doch ein einigermassen klares
Bild der ursprünglichen Vegetation. Ein interessantes Gemisch der
Vertreter verschiedener Vegetationsformationen fand sich. Ähnlich
wie auch bei uns mischten sich zu der Kalkheide typische Vertreter
der Wiesenvegetation wie auch solche der sonnigen Hügel und der
Waldvegetation. *Ilex* und *Fraxinus* z.B. wuchsen dort einträchtig-
lich mit *Gentiana amarella, Bellis perennis, Plantago lanceolata,
Dryas, Sesleria cærulea, Kœleria cristata, Carex pulicaris, Hypericum
pulchrum, Arctostaphylus, Ulex,* etc. Wie auch bei uns konnte man
leicht nachweisen dass die Wurzeln der *Calluna*, wie auch der
übrigen Heidepflanzen, unter der oft dünnen Humusdecke direkt
auf den Kalk auflagen, resp. an ihm. hafteten. Selbst der von
Kalkresten durchsetzte untere Teil des Heidehumus brauste bei
Zusatz von Salzsäure auf.

Das massenhafte Vorkommen von *Eriocaulon* in den Seen des westlichen Irland weist auf eine bisher nicht genügend geklärte pflanzengeographische Eigenart der Britischen Inseln hin. Der vortreffliche Forscher der Englischen Wasser- und Sumpfpflanzen, A. Bennett, hat nachgewiesen, dass England mehrere den Nord-Amerikanischen zum mindesten sehr nahestehende *Potamogeton*-Arten besitzt. Die berühmte *Spartina*-Formation in Süd-England passt trefflich in diesen Rahmen. In Mitteleuropa sind solche Anklänge an die Amerikanische Flora, soweit sie nicht nur durch den Menschen veranlasst wurden, recht selten. Vielleicht gehört in diesen Rahmen das ganz isolierte Vorkommen von *Kalmia angusti-folia* in einem Moore bei Hannover.

Ganz besonders imponierend für den Bewohner der trockneren Mitteleuropa ist die typisch Atlantische Vegetation des westlichen England und namentlich des westlichen Irland. Während wir in Deutschland in den Gebirgen höchstens in den feuchten Schluchten der regenreicheren Hänge etwas wie eine echte Epiphytenflora finden, kommt in Norddeutschland höchstens einmal hie und da spärlich *Polypodium vulgare* auf den unverletzten Aesten alter Eichen in den Dünentälern der Ostsee vor, und auch diese anspruchslose Pflanze meist in recht kümmerlicher Entwickelung. Dass die Zahl der oft in Astlöchern etc. wachsenden " Überpflanzen " sehr gross auch in Deutschland ist, ist bekannt, aber diese mit ihren Wurzeln in dem geschützten Inneren des hohlen Stammes steckenden Pflanzen hängen eben nicht von den kleineren Perioden des Klimas ab wie die echten Epiphyten, deren üppige Entwickelung bei Killarney fast an tropische Verhältnisse erinnert. Die dicken Moospolster, besonders von *Hypnum cupressiforme* u.a., die die Eichen und auch Eschen bis fast auf den Gipfel bedecken, geben den Farnen und auch anderen Pflanzen beste Gelegenheit zum üppigen Gedeihen.

Auch die übrigen Pflanzen, die die dort dauernd herrschende feuchte Luft lieben, zeigen eine zum Teil ungeahnte Entwickelung. In den üppigen Wäldern, in die sich z.B. die mediterrane *Arbutus unedo* in Pracht-Exemplaren einmischt, sind oft mehrere Etagen von Unterholz übereinander ausgebildet, eine Erscheinung, wie sie sich eben nur in solchen Klimaten findet. Professor Lindman machte mehrmals auf die veränderte Tracht des *Pteridium aquilinum* aufmerksam, welches nicht, wie bei uns auf dem starren Stiel stehende Blätter besitzt; sondern nach Art tropischer Farne mit seinem verlängerten Mittelstreif und dem

starr abstehenden Fiedern klettert es als " Spreizklimmer" in die
Höhe der Sträucher. *Ilex aquifolium* sehen wir bis zum Umfange
von 1·05m., *Arbutus* bis 1·8m. in 1m. Höhe, *Calluna* hatte im
lichten Walde eine Höhe von mindestens 1·2m., einige bis 1·8m.
und noch mehr; eines desselben, mit dem Professor Massart
mich photographierte, hatte die stattliche Höhe von 2·2m.! Auch
Blechnum spicant war bis 7 dm. hoch. Dies seien einige der
characteristischten Beispiele der Aufzeichnungen von besonderer
Üppigkeit in jenem Klima, welches den zierlichen *Hymenophyllum* das
üppige Gedeihen gestattet. Dass auch die Pflanzen anderer
Vegetationsformationen hier ungeheure Grössen erreichen beweist
die beobachtete Höhe von *Schœnus* von 1·15m. Cornwall besonders
der Lizard schliessen sich dem ebenbürtig an.

Aber nicht nur die grosse Üppigkeit der Vegetation des warmen
Westens bietet dem Pflanzengeographen grosses Interesse, die
grossen pflanzengeographischen Contraste geben manches Rätsel
und manche Aufklärung. Rätsel, soweit es schwer ist für ihr
Vorhandensein eine stichhaltige Erklärung zu geben, Aufklärung,
als manche scheinbaren Widersprüche aus postglacialen Funden,
etc., durch sie verständlich werden. Das feuchte Klima scheint in
vielen Fällen pflanzengeographische Contraste völlig auszugleichen.
Schon das Vorkommen des xerophytischen *Sedum anglicum* in einem
Rasen der Repräsentanten der hygrophilsten Vegetation *Hymeno-
phyllum peltatum*, welches Frau Praeger bei Killarney fand, findet
wohl kaum ein Analogon bei uns.

Das auffälligste ist aber doch das Vorkommen der *Dryas octo-
petala* mit den zahlreichen Vertretern der südlich-atlantischen Flora
in westlichen Irland, und namentlich ihre Berührung an denselben
Standorten bei Ballyvaghan mit *Adiantum capillus-Veneris*. Da
selbstverständlich in unmittelbarer Nähe dieser Standorte, am
Fusse der betreffender Hügel auch unsere Waldbäume und ihre
Begleiter wachsen, so können und müssen noch heute solche von
den norddeutschen so völlig verschiedener Ablagerungen des "*Dryas*-
Horizontes" mit ihrer Beimischungen zustande kommen, wie sie
von den Britischen Inseln beschrieben wurden. Das Klima muss
schon in jener Zeit wesentlich von den norddeutschen verschieden-
gewesen sein. Auch ganz anderen Pflanzengenossenschaften
vermag sich *Dryas* dort anzupassen, so fanden wir es auch in
Gesellschaft der *Plantago maritima*.

Ein weiteres sehr auffälliges Moment, welches unseren
dortigen botanischen Freunden die Frage nach dem Indigenat

vieler Pflanzen sehr erschweren muss, ist die Leichtigkeit mit der
viele Pflanzen verwildert und eingebürgert sind. *Acer pseudo-
platanus* wurde schon vorher erwähnt. *Cotoneaster microphylla* und
auch *Symonsii* sieht man vielfach an Mauern und Eisenbahn-
dämmen gleich einer heimischen Art. *Escallonia macrantha* sieht
man in West-Irland oft weit von aller Cultur. *Mesembrianthemum
acinaciforme* hängt in langen Polstern an den Felsen von Lizard
Point. *Rhododendron ponticum* is an vielen Orten des Vereinigten
Königreichs zur völlig heimischen Pflanze geworden: bei Killarney,
etc., macht die Art der indigenen Vegetation erfolgreiche Concurrenz
und verändert die Physiognomie der Wälder völlig.   Bei Cally
unweit Dunkeld mischt sich das capensische *Aponogeton distachyum*
in grosser Menge mit den heimischen Wasserpflanzen.   Das
imposanteste Beispiel beginnender Einbürgerung waren aber die
zahlreichen jungen Pflanzen der *Dicksonia antarctica*, die als
Sämlinge der von Mr. P. N. Williams in seinen herrlichen und hoch-
interessanten Park gepflanzten Baumfarne aufgegangen waren.
Letztere waren zu so prachtvoller Entwickelung gediehen, dass ihre
natürlichen Standorte auf der südlichen Halbkugel kaum schöner
sein können.   Sehr bemerkenswert ist auch die massenhafte
Verbreitung der *Fuchsia Riccartoni* besonders bei Clifden (West-
Irland) die als Bastard nie eine Frucht bringt, und doch kilo-
meterweit die Wege begleitet, sich mit *Dabeocia, Ulex Gallii,* und
den atlantischen Ericaceen mischt.   Auch *Montbretia crocosmiiflora*
die wir mehrfach zahlreich trafen, vermehrt sich wohl in Wesent-
licher vegetativ.

VIII—SOME IMPRESSIONS AND REFLECTIONS.

BY F. E. CLEMENTS (Minneapolis).

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AS one of those deeply interested in the structure and develop-
ment of vegetation, I shall leave to other members of the
party the difficult but pleasant task of doing justice to scenic
Britain and to British hospitality.   I shall confine myself to
sketching the kaleidoscopic impressions of British vegetation, with
an occasional reference to the interpretations arising out of
comparisons with American vegetation.

The three days spent in the Norfolk " Broads " revealed the
general features of a fascinating succession with an unusual
number of structural and developmental problems.   The striking
alternation of *Scirpus, Typha, Phragmites* and *Cladium* affords
unique opportunity for the study of their habitat equivalences and
re-actions.   It would be difficult, if not impossible, to find a region
quite so favourable for such work, owing to the labyrinthine nature
of the " Broads," beside which the fabled labyrinths of Crete seem
mythical indeed.   In the case of the submerged and floating
populations, the light and aëration factors furnish an almost
untouched field, while on the other side, historically, of the reed-
swamp plexus, stretch the problems of its conversion into fen and
carr.   The ecotone between swamp and fen is an unusually broad
one, with corresponding possibilities for studying the change of
dominance in relation to habitat factors.

At Blakeney, the vegetational interest centred in the sharp
contrast between the salt marshes and the shingle beach, which
both makes the marshes possible and then overwhelms them.   As
a dynamic center, the shingle bank is rivalled only by the sand
dunes, though it seems to differ in being rather more periodic than
continuous in growth.   The production of new habitats for coloni-
zation rarely occurs in such a rapid manner, while the periodic
development of lateral banks would seem to furnish a unique basis
for the study of the sequence of different populations, both
on shingle and in the marsh.   The quantitative study so charac-
teristic of British ecology, finds perhaps its best exemplification at
Blakeney, where also the refinements of exact methods can be
carried further than in more complex regions.

English woodlands are an intricate puzzle to the American

ecologist familiar with little else than natural forests, rarely changed except through fire or the hands of lumbermen. The control by man has been so long and continuous and the effect of grazing and of rodents so significant that one is inclined to suspect all comparisons with the virgin forest formations of America. The very fact that continuous stretches are rare further complicates the task. Naturally one finds many phenomena which he would interpret in terms of native vegetation, but this is gratuitous until further quantitative study has been made of the respective ages of different woody populations, the relative dominance of woodland, scrub and grassland, and the actual inter-relations between vegetation and habitat.

The problem of the moor, with its scientific, economic and practical aspects, appeals to the visitor as the outstanding problem of British vegetation. The divergent opinions among European botanists as to the nature of moor and its variations, of its relation on the one hand to swamp and fen, and on the other to heath, constitute a situation in which the American, unfamiliar with these formations, finds it impossible to discover definite landmarks. He realizes, however, that there is here an almost unparalleled opportunity for recording the movements from year to year, in addition to securing fundamental evidence by the methods of experimental vegetation. To one impressed with the complex relations between moor and heath, "Hochmoor" "Flachmoor" and fen, it seems that an exact study of all the factors and population changes for a long period will be necessary for a solution. The importance of doing this is greatly emphasized by the widespread opportunities for tracing the vegetation movements of the past in the almost innumerable peat sections. These serve as an invaluable link between the successions of to-day, and of the immediate geological past. It seems beyond question that their thorough study will reveal much of the development and structure of vegetation long since disappeared. British botany contains no more alluring field than this of correlating the peat deposits and connecting their successions with those in existence at present.

It is, perhaps, not altogether idle to speculate in regard to the reclamation of the moors. Their wide extent and almost complete lack of use, mark them as an asset of great economic importance, and one must be allowed to indulge the hope that the British Vegetation Committee will soon take steps towards the conquest

of the moor practically, as well as ecologically. One must believe that research is of value only as it broadens and deepens the current of human progress, and that no one should be so well qualified to apply the results of investigation as the man who obtained them.

To one sceptical as to the influence of lime, the results of the Excursion were most interesting. One could not fail to be impressed with the abundant evidences of the distributional significance of lime, while he was struck by the fact that scarcely a single " calciphilous " or " calciphobous " plant could prove a clear title to the term, physiologically. It is useless to add a single line to the literary solution of this hoary problem, but the British experience serves to emphasize the conviction that nothing but physiological and competition studies in the field can hope to lead us to a final solution.

Without doubt, the greatest personal return from the Excursion was the first-hand insight into the point of view of ecologists from different countries, and the chance thus afforded of scrutinizing one's own concepts in the light obtained. This must be more and more the real value to be derived from such experiences, if they are to give more than individual benefits, as they will. Botanists, like all scientists, are still so highly individualized that they have little sympathy or patience with anything which looks toward definite and effective co-operation. This would seem to be merely an intermediate stage, and we can hope for the time when the ecologists of many countries will work together with something of the unity and efficiency which characterize the British Vegetation Committee.

THE
PLASMATIC MEMBRANE AND ITS ORGANISATION.

By F. F. Blackman.

F. Czapek. "Über Fällungsreaktionen in lebenden Pflanzenzellen und einige Anwendung derselben." Ber. deut. bot.Ges., Bd. XXVIII, 1910, pp. 147–159.

,, "Versuche über Exosmose aus Pflanzenzellen." Ibid, pp. 159—169.

,, "Über die Oberflächenspannung und den Lipoidgehalt der Plasmahaut in lebenden Pflanzenzellen." Ibid, pp. 480—487.

,, "Über eine Methode zur direkten Bestimmung der Oberflächenspannung der Plasmahaut von Pflanzenzellen." Jena, Gustav Fischer, 1911, 86 pp.

W. W. Lepeschkin. "Zur Kenntniss der Plasmamembran." Ber deut. bot. Ges. Bd. XXVIII, 1910, pp. 91—103.

,, "Zur Kenntniss der Plasmamembran. II," Ibid, pp. 383–393.

,, "Zur Kenntniss der chemischen Zusammensetzung der Plasmamembran." Ber deut. bot. Ges., Bd. XXIX, 1911, pp. 247—260.

,, "Über die Einwirkung anæsthesierenderer Stoffe auf die osmotischen Eigenschaften der Plasmamembran." Ibid., pp. 349—354.

IT has long been recognized that the surface-layer of any mass, whether solid or liquid, differs somewhat in physical properties from the internal parts of the mass. This physical difference is of course related to the fact that the molecules of the surface-layer have molecules of their own nature only upon one side of them, and they are therefore in a different environment from more centrally situated molecules, as regards the distribution of the inter-molecular forces.

This general principle applies also, of course, to the mass-units of living things, the individual protoplasts and indeed very special properties, for example in the matter of selective permeability, are generally attributed to the "Plasmahaut" or surface-layer of the protoplast.

It is very interesting to find two such trenchant investigators as Czapek and Lepeschkin now converging upon this same subject—the organisation of the plasmatic membrane—by two quite independent lines of work. After some general remarks upon the biochemical aspect of the matter, I propose to give a summary of the progress that has been made by each of these workers.

I.—The Physical Chemistry of Surfaces.

The purely *mechanical* result of the special condition of the surface-layer of a mass of solid or liquid is the same as if we imagine the existence of an elastic skin compressing the mass and tending to deform it until the skin attains the smallest surface possible under the circumstances. The skin thus exerts a surface-tension, and energy is liberated when the skin contracts, and absorbed when the skin is caused to extend.

When this surface-tension has a negligible effect on the form of the mass, the substance is said to be a solid, but liquid if the surface-tension predominates over the resistance of internal friction, so that a particle otherwise unconstrained takes the spherical form, which gives the minimum possible surface for the volume. Of known liquids water has the highest surface-tension at ordinary temperatures, and as a purely physical factor the effect of this property enters into a number of biological phenomena.

This physical state of the surface-layers of a liquid has, however, a still more profound effect in the modification which it induces in the *chemical processes* taking place in these layers. Such surfaces are to be regarded as being the seat of a special form of energy, which is termed "surface-energy," and it is this surface-energy which is liberated on contraction and becomes latent in expansion of the surface.

The presence of surface-energy in the superficial layer affects the chemical processes taking place there in a way quite analogous to the way in which temperature, or pressure, or electrical energy, affect chemical processes. This has been clearly formulated by Ostwald, who, in the last edition of his " General Chemistry," devotes a special section to what he calls " Microchemistry,"[1] or the chemistry of small masses. The smaller a mass of matter, the greater is the proportion of its surface to its volume and the more the chemical processes conditioned by surface-energy dominate over the ordinary processes, which are conditioned by volume-energy and take place throughout the rest of its mass. When a drop of water has only a diameter of about 1μ (which is near the limit of microscopic vision), then even its density is perceptibly greater than unity and the surface-energy effects are quite

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[1] Third English Edition, translated by W. W. Taylor (MacMillan, 1912). To such an act of piracy with regard to a term with a long-established different use in biology we can only submit without protest, in respect for the chemical philosopher to whom science owes so much.

marked. Still more marked are these effects when the same volume of water is stretched into a film, or better into a thread, for then the relation of the surface to the mass is still further increased.

The purest natural manifestation of micro-chemical effects occurs when two different substances are intimately mixed, the particles of one being distributed in a liquid medium of the other, as in suspension and emulsion colloids. " Kolloid-Chemie " has naturally, then, become quite a separate branch of investigation, with its own specialists and its own journals, and this is so because surface-energy, due to the enormous surface presented by the colloid particles, is always the conditioning energy of the chemical processes in colloids. In Ostwald's terminology colloidal chemistry is the typical part of Microchemistry, and the characteristic chemical changes are those that are grouped as *adsorption*; to these belong dyeing and many other technical processes. Such are governed by special quantitative laws, which make the process of adsorption intermediate between physical absorption and chemical union. The physical chemistry of toxins, antitoxins, agglutinins, etc., illustrate the complexity of the quantitative laws holding in this field.

Of peculiar importance in " microchemistry," is the law governing the spatial distribution of dissolved substances which alter the surface-tension of the water in which they are dissolved. Established on thermo dynamical considerations by Willard Gibbs in 1878, this law is generally known as "Gibbs' theorem ": developed also by J. J. Thomson in 1887, it has been called by Macallum[1] the " Gibbs-Thomson rule." According to this rule substances in solution, which tend to lower the surface-tension of the solvent must accumulate in the surface layers, and this local accumulation will increase until the work done against osmotic pressure equals that gained by diminution of surface-tension and a state of equilibrium is arrived at. Substances which tend to raise the surface-tension will be repelled from the surface, and will be less concentrated there than in the general mass of the solution.

Colloid particles, having very slight osmotic pressure, will

[1] British Association Reports, 1910. Presidential Address to Section I. In this address Macallum elaborates the part that surface-tension may play in the functioning of animal organs, and correlates his studies of the localisation of salts in the cell with the Gibbs-Thomson rule.

be able to accumulate more strongly at the surface than the true solutes, as the force redistributing them will be slighter. Sugars have only a very slight effect on surface-tension ; salts, which raise surface-tension, will be repelled from the surface ; while proteids and fatty substances which lower surface-tension, will accumulate at the surface and tend to form a more concentrated layer. Of these substances, the fatty substances (lipoids), including neutral fats, soaps, lecithin, cholesterin, etc., lower surface tension very much more than do proteids, and so they will be relatively more abundant in the surface layers.

There is no way of ascertaining the thickness of the superficial strata affected by this surface-concentration, but it is below the limit of microscopic visibility, and Ostwald states the special surface-properties of a drop of water extend only to depth of about one millionth of a millimetre.

The application of these general principles of surface-action and micro-chemistry to the living cell may be postponed till we have reviewed the contributions of Czapek and Lepeschkin to our knowledge of the plasmatic membrane.

II.—Czapek's Researches on the Plasmatic Membrane.

The four papers by Czapek referred to at the beginning of this article make a most interesting series in which we find an admirable prosecution of a line of investigation, ending in the discovery of a new general attribute of living plant-cells. The first paper sets out the details of a study of the precipitates that can be produced inside the living cell by certain agents of a basic nature. Charles Darwin, in 1876, described the phenomenon of " aggregation " in the red cells of the tentacles of *Drosera*, that was produced by dilute ammonia. On application of this agent, fine red drops appear in the cells and these run together to bigger globules and may ultimately form one large irregular "myelin-like " mass in each cell. Loew and Bokorny showed similar colourless aggregation in the mesophyll cells of *Echeveria*, and found that caffein (0·2% solution) is better than ammonia for producing them. Czapek has extended their observations and finds that practically all plant-cells that contain tannin give this effect and that cells containing the tannoid substance anthocyan are the easiest for observation,

The appearance of the precipitate suggests a fatty substance, but by careful tests Czapek shows that the bulk of it is a loose

compound of tannin and caffein, which slowly hydrolyses and disappears when left in water.

Spirogyra gives this precipitate well, except when it is poor in tannin, and in *Spirogyra* it can be seen that the precipitate forms partly in the vacuoles and partly in the cytoplasm.

Certain other bases such as baryta give an analogous compound, but soda and potash fail to work because the Na. and K. ions do not penetrate the protoplasm. Czapek states that *Echeveria* gives an obvious deposit with ammonia so dilute as 1 mole in 15,000 litres, so that it is three times as delicate a test for ammonia as the much vaunted Nessler's test.

In the second paper it is noted that substances which injure the protoplasm, as chloroform and acids of sufficient strength bring about the exosmosis of the contained tannin, so that the cells no longer give the conspicuous myelin-formation when treated with caffein. If all the tannin has not escaped, a fine granular precipitate may arise in the cells, or perhaps only a brownish turbidity. It is clear then that we have here a convenient reaction for testing the effect of various water-soluble substances upon the permeability of the protoplasm, as exemplified by the exosmosis of the tannin. This study Czapek then took up, with important results. He tried a great range of the stronger acids and found that they all produced exosmosis at the same critical concentration. If the acid is more dilute than 1 mole in 6,400 litres, no exosmosis results even after many hours, but at this particular strength appreciable exosmosis begins and the tannin steadily escapes, so that after some eighteen hours in acid, caffein no longer produces a precipitate, and, indeed, the tannin can be detected in the solution outside the cell.

An extremely interesting coincidence lies in the fact that Kahlenberg and True, in 1896, found exactly this strength as the minimum which inhibited the growth of roots submerged in dilute acids of various kinds. No doubt the increased permeability of the cells of the root-tip inhibited their efficiency as growing units.

Czapek then tried the effect of other organic solutes upon the exosmosis of tannin, using chiefly the mesophyll of *Echeveria* as standard material. Thick sections are laid for twenty-four hours in the solution to be tested, then washed and placed for at least one hour in a drop of 0·2% caffein in a damp chamber. At the end of this time the cells are examined with the microscope and the amount of precipitation noted.

All specific poisons which kill the cell cause, naturally, exosmosis, but a large number of organic substances which are not specific poisons, such as alcohols, esters, etc., cause exosmosis in sufficient concentration.

In a homologous series like the monovalent alcohols the critical concentration required diminishes rapidly as the series is ascended : methyl alcohol, 15%; ethyl, 10%; propyl, 4-5%; butyl, 1-2%; amyl, 0·5%.

Now Traube, in 1904, got together evidence to show that the toxicity of these subtances increased in this way for animal tissues and that the effect of the different homologues in lowering surface-tension increases exactly *pari passu*. Each successive member of the series becomes three times as toxic and three times as depressant of the surface-tension when dissolved in water. It therefore looks as if the production of exosmosis is closely correlated with surface-tension of the liquid in which the cell is bathed.

Czapek subsequently proceeded to determine the surface-tension of a great variety of organic substances in solution, and at the same time try their effect as producers of exosmosis.

He determined the surface-tension in the simplest way by seeing what resistance the liquid offered to the formation of air-bubbles on pressing air through a capillary tube submerged in the solution. The head of pressure required to cause bubbles just to escape from the mouth of the capillary tube of his " capil–larity-manometer " gives a measure of the relative surface-tension of the solution employed.

The correlation between surface-tension and exosmosis was most striking and unexpected, for it was found that *if any organic substance whatever is dissolved in water in sufficient amount to lower the surface-tension to 0·68* (pure water being taken as unity) *then this solution just brings about exosmosis from the cell.* There is thus established a new principle of great fundamental importance. The cell's power of retaining its contents is a matter of physical organisation of the superficial layer, and these substances which upset the power do so, not by virtue of any chemical action on the protoplasm, but by some surface-tension relation.

Specific poisons, which cause exosmosis in much weaker concentrations no doubt act *chemically* on protoplasm (and indeed many of these do not lower, but raise, surface-tension), but this physical action now discovered is a quite general one, without exceptions. No case was found of the cells of a flowering plant

being able to retain their contents in a medium of lower surface-tension than about 0·68.

In his third paper Czapek proceeds to point out the simplest explanation of this general rule is that the living cells of higher plants have actually a surface-tension of this particular value, 0·68.

Now as mentioned in the introduction it has been shown by Willard Gibbs on thermo-dynamical grounds that if substances which lower surface-tension are dissolved in a liquid they must accumulate in the surface-layer, and that those substances which lower it most will displace any less active ones. Czapek concludes therefore that the exosmosis is caused by the new substances brought into contact with the protoplast being taken up by the surface-layer and displacing the normal contents; whereby in some way a greatly increased permeability is produced and exosmosis starts at once.

Czapek then turned his attention to *colloids*, as it had been long known that colloidal emulsions of fats, soaps and other lipoid bodies in water have a very low surface-tension. These emulsions followed exactly the same law as the true solutions and any lipoid emulsion with a surface tension as low as 0·68 caused exosmosis. One significant point emerged, namely, that a strong emulsion of a neutral fat in water has a minimal limit for its surface-tension, which is not passed however strong the emulsion, and this limit is just about 0·68. We are irresistibly driven to think of the theories of Quincke, Overton and Meyer, which assumed the presence of fats in the surface-layer of the protoplast. Grant the surface-layer of the protoplasm to be a saturated emulsion of some neutral fat and its surface-tension and relations to exosmosis thereby are made comprehensible.

The lipoid theory of the plasmatic membrane, based, so far, on amœboid movement, the selective uptake of aniline dyes and the narcotic action of fat-solvents, thus gains strong support from these researches on surface-tension.

In his fourth publication Czapek discusses the probable nature of this surface-layer more in detail and points out that there are no grounds for assuming a continuous fatty film round the cell, but that an emulsion containing only a few parts per cent of fat would give all the required properties. The fat would be suspended as an emulsion in perhaps a continuous colloid complex of water and proteid, and thus the uptake of substances insoluble in

fat and soluble in water, like the salts and sugars which form the basis of metabolism, would be easily understandable, whereas on the older view there was a complete *impasse* in this direction. Present developments of these views give no clue to why some water-soluble substances are taken up by the cell and others not. In his pamphlet Czapek gives a long list of parts of flowering plants which serve to demonstrate this genera relation of surface-tension and exosmosis; and among them there are no exceptions to the 0.68 rule.

Yeast, however, requires a lower surface-tension down to 0·5 or 0·6 to bring about exosmosis of its invertase, and here it may be that lecithin or cholesterin is the lipoid in its surface-layer, as these two have just such a very low surface-tension in solution. Whereas 10% ethyl alcohol causes exosmosis in higher plants, 15% is needed for yeast, and the same is true for the exosmosis of hæmoglobin in hæmolysis of red blood-corpuscles.

Czapek also discusses in some detail the action of narcotics on which Overton based his lipoid theory, but that matter cannot be gone into here. It must be pointed out that Overton finally assumed the activity of lecithin and cholesterin in the normal plasmatic membrane, but the new evidence seems to favour the presence, not of these particular lipoids, but of neutral fats, except in the case of yeast, and no doubt some other lower organisms.

III.—LEPESCHKIN'S RESEARCHES ON THE PLASMATIC MEMBRANE.

Concurrently with the publication of Czapek's four papers there appeared four papers by Lepeschkin approaching the same subject from quite a different point of view.

In 1906 Lepeschkin began researches upon the permeability of protoplasm, being led to these by his excellent study of the mechanism of water-secretion in *Pilobolus*. A number of papers which followed this work dealt with alterations of the degree of permeability of protoplasts as a factor in modifying cell-turgor and the production of movements in *Mimosa* and in nyctitropic plants.

To these were added papers on turgor and permeability in relation to growth, and finally in 1910 and 1911 the four papers now to be considered, dealing directly with the constitution and organisation of the plasmatic membrane.

We may take first the new experimental work that is contained in these papers and postpone till afterwards the theoretical views and detailed discussion of the physical organisation of the plasma-

membrane. The first lot of experiments dealt with the coagulation
of the " Plasmamembran "[1] which can be brought about by different
agents and the light which such action throws upon the nature of
the membrane.

Heat-coagulation of the plasma-membrane. It is a characteristic
of proteids alone among colloids to coagulate at sharply defined
temperatures and the fact that protoplasm exhibits this property is
strong evidence of the dominance of proteids in its organisation.[2]
If a plasmolysed cell of *Spirogyra* be slowly heated while under
observation with the microscope the coagulation is made evident by
the change from a smooth shining appearance of the plasma to a
dull granularity. This takes place in a few seconds when the right
temperature is reached, and there is also obvious increase of perme-
ability, for the protoplast rapidly shrinks by escape of its contents.
In *Spirogyra* the average temperature of coagulation is $50.5°C$ ($\pm 1°$
C). If the red epidermal cells of *Tradescantia* be plasmolysed with
sugar and then heated up, strong shrinkage at 70.7 marks the
moment of coagulation and increased permeability; as the anthyo-
cyan does not escape till the coagulation is quite complete there
results at first a visible deepening of the cell colour. It is interesting
to find that if the same material be plasmolysed with glycerine, which
penetrates the protoplast fairly easily, then there is a strong increase
of volume at the moment of coagulation, instead of contraction.
Further work provides a clue as to why the above two coagulation-
temperatures are so far apart. This depends on the fact that the
Spirogyra protoplast is acid and *Tradescantia* alkaline and it can be
shown experimentally that a trace of acid ($.1\%$ citric) added to the
plasmolysing sugar lowers the coagulation-temperature, while a trace
of alkali ($.1\%$ Na_2CO_3) raises it. With *Spirogyra* the acid may
lower the temperature $5°C$ from the normal and the alkali raise it
$5°C$. With *Tradescantia* in the acid medium the coagulation-

[1] Throughout his papers Lepeschkin uses the term "Plasma-
membran" for the structure he is investigating. He regards
this as including the superficial layer of the protoplast and an
unknown depth of the underlying strata, *possibly the whole
thickness*, for he will not commit himself to any definition of
the Plasmamembran except that it is the layer which is the
seat of the selective permeability.

[2] The conception of the relation of coagulation of proteins to
temperature and the presence of acids and alkalis here given
is that current a few years ago. Recent studies on the nature
of the mechanism of heat-coagulation of proteins by Dr.
Harriette Chick and Dr. Martin have raised onr knowledge
to an altogether higher plane (see Journal of Physiology, Vol.
XLIII, and British Association Report, 1911, pp. 281—286).

temperature is lowered to 60·6°C, not very far removed from *Spirogyra* in alkaline medium. These effects of acid and alkali are thus in accordance with their effects on coagulation of proteids 'n vitro.

Incidentally Lepeschkin noted the interesting fact that the chloroplast of *Spirogyra* can be seen to coagulate at about 48°C; more than 2°C below the temperature coagulating the cytoplasm.

Coagulation of plasma-membrane by mechanical stress. In non-living colloids coagulation by pressure has not yet been observed, but it is apparently quite easily produced in the cytoplasm of *Spirogyra*. It is not difficult to imagine that in a sufficiently complex colloidal structure, sudden pressure, which brought into contact the otherwise dispersed colloid particles, would lead to interaction between them resulting in their aggregating to larger masses, which is the essence of coagulation.

Sudden pressure on filaments of *Spirogyra*, sufficient to rupture the cells, generally leads to complete coagulation of the cytoplasm. More gentle pressure first of all coagulates only the outer layer, and if the cells be previously plasmolysed this effect is very easily observed by the change of appearance of the plasma-membrane, such as was described for heat-coagulation.

If a *Spirogyra* filament is kinked at one spot by being lifted up on a glass thread, local coagulation is produced just there and when the filament is subsequently plasmolysed the protoplasm is seen to be sticking to the wall at that spot, while pushed back else-where by the plasmolysing solution.

Lepeschkin considers that he has seen recovery take place from small local spots of coagulation of the outer layer of plasmo-lysed cells, a very important indication of vital organisation tending to maintain the fluid condition of the protoplasm. Complete coagulation leads to chemical change and is thereby irreversible, being one of the chief causes of " death " of the cell.

Even the stress of rapid plasmolysis and deplasmolysis may be sufficient to coagulate the protoplast, and the more rapidly these processes are carried out, the more effective they are in coagulation. Acids and alkalis have the same effect upon the susceptibility to mechanical stress as upon susceptibility to temperature. Thus a certain treatment of plasmolysis and deplasmolysis which coagulated 76% of the cells of *Spirogyra*, only coagulated 6% after three-and-a-half hours in ·05% Na_2CO_3; whereas in another case preliminary treatment with ·01% citric acid doubled the percentage of coagulated cells.

The naturally alkaline *Tradescantia* is very resistant to the strain of plasmolysis unless first treated with dilute acid.

Coagulation by chemical agents. As confirmatory evidence of the dominance of proteids, Lepeschkin shows that organic substances like alcohol, aldehyde, chloral, act upon the typical protoplast in the same way as upon egg-albumin. The concentration of each of these substances required to produce complete coagulation of egg-albumen in ten minutes is practically the same as that required to coagulate the plasma-membrane in ten minutes.

Further, alcohol lowers the temperature of coagulation of both egg-white and *Tradescantia* protoplast in a similar way, for which detailed temperatures are given in the paper.

The presence of lipoids in the plasma-membrane. Like Overton, Czapek and others, Lepeschkin finds evidence that lipoids are present in the plasma-membrane, but he dissents from Overton's view that such bodies form a continuous film on the surface of the plasma and are the only intermediaries in selective absorption.

According to Lepeschkin, if lipoids are present in the plasma-membrane, then the presence of these active absorbers of narcotics should bring it about that less strong watery solutions of narcotics would be required to coagulate this membrane than to coagulate the simple proteid of white of egg. While the coagulation of the two media by alcohol or aldehydes was found to require similar concentrations; for narcotics like ether only one-third, for chloroform one-eighth, and for thymol one-thirtieth of the concentration coagulating white of egg suffices to coagulate the plasma-membrane. It will be noticed too that the more soluble the narcotic is in lipoids in comparison with water, the more abundantly it is taken up and the more effective it is on the plasma compared with pure proteid; ether is 4·5 times as soluble in oil as in water, chloroform 30, times and thymol more than 100 times).

If the lipoids do not form a continuous film over the cell they might be present as an emulsion or loosely combined with the proteids of the plasma. The last is Lepeschkin's view and such lecithin-protein complexes are certainly known.[1] Nathansohn started the hypothesis that the surface-layer might consist of a mosaic of lipoids and living protoplasm (proteid) independently responsible for the uptake of substances soluble in fats and in water

[1] Handovsky & Wagner, Broch. Zeits. XXXI, 1911, p. 32.

respectively. Lepeschkin provides evidence against this view by showing that the entry of water-soluble dyes and salts is diminished by the presence of narcotics, so that the lipoid and watery elements are not independent.[1]

Thus *Spirogyra* takes up enough methylene blue from a very dilute solution to be appreciably coloured in forty minutes, but if kept narcotised by $2\frac{1}{2}\%$ ether, added to the blue solution, then there is no colouration in forty minutes, this dye being rather insoluble in ether. If bismarck–brown is employed instead, which dye is very soluble in ether, then narcosis does not diminish the amount of stain taken up. On the uptake of any dye by dead cells, ether has no effect.

Similarly by comparison of the isotonic coefficients for potassium nitrate and cane sugar in plasmolysing *Tradescantia* epidermis, it is found that the permeability to the salt is much diminished in etherised cells in the ratio of 11 to 7. In ether-narcosis, diminished permeability leads to increased turgor, and *Spirogyra* filaments are accordingly found to increase $0\cdot1\%$ in length when placed in $2\frac{1}{2}\%$ ether solution.

Scattered up and down these four papers are a number of discussions and criticisms which bear on the constitution of the plasma membrane, and we may now give a summary account of Lepeschkin's views on this subject.

The plasma-membrane is defined as the part of the protoplast which determines the selective permeability, but it is left an open question as to whether this is a thin superficial layer, or the whole thickness of the protoplasm. Various lines of evidence and Lepeschkin's own coagulation experiments, however, prove that a visible outer layer has a less stability than the mass of the protoplasm.

The plasma-membrane is obviously a complex colloidal structure and its selective permeability only holds while it is " alive." It is fluid in nature, yet will coagulate spontaneously in time, like the temporary fluid phases of many inorganic precipi-

[1] Much of this argument is very fine-drawn and we have not sufficient physical knowledge yet to reason closely about the properties of such a complex surface-layer as the protoplast may possess. Quite recently Hardy (Royal Society, May 16th, 1912) has discussed the properties of a *composite* oil and water surface.

tates.[1]   Senility brings on spontaneous coagulation and so do certain physical and chemical treatments.   Heat, pressure and deformation by plasmolysis are agents of the first class ; and salts of heavy metals, acids, alcohol, etc., represent the second class.

The way in which these agents act is such as to indicate that proteids are the dominant constituent of the plasma membrane.   As its outer surface does not mix with water, the membrane cannot be colloid particles distributed in a water medium, but the con- tinuous medium must be something else which can imbibe water without dissolving in it—probably a proteid with water imbibed in it, and also with particles of water distributed through it as an emulsion-colloid.

On coagulation the proteids aggregate to form large particles and the water runs together to form fine canals through which non-selective permeation readily takes place.

On general principles, penetration of such a living membrane by any given substance must depend on the solubility of the substance in the continuous medium and it would seem that it should not be entirely impenetrable to any water-soluble crystal- loid.[2]

Lepeschkin draws attention to an important flaw in the evidence held to prove the impenetrability of many dyes soluble in water.   Unless such a dye unites with something inside the cell and is therefore *cumulatively stored* there can be no visual evidence as to whether it penetrates or not, for the colour of the unconcen- trated solution is too pale to be visible in the cell.

[1] A number of precipitates of colloid substances are, when first formed, spherical drops of fluid containing much water, and they only become solid granular aggregates after some time. Quincke showed that copper ferrocyanide when first pre- cipitated is liquid, but it sets solid in a few seconds. Lepeschkin added 90% alcohol to 20% ammonium sulphate and found that a cloud of drops separates, crystallising only after some hours. Like the setting of plasma this solidification is hastened by mechanical stress.   Similar drops of liquid precipitate are formed when saturated am- monium sulphate is added to 20% albumose, and these drops coagulate spontaneously in time.   These drops of liquid pro- teid behave not unlike protoplasts in that they become vacuolated in salt-free albumose solution by taking up water. They then show selective permeability in that they can be shrunk to almost nothing (plasmolysed) by immersion in strong sugar solution, while saturated potassium nitrate penetrates too fast to plasmolyse them.

[2] New important relations between the size of their colloid par- ticles and the uptake of aniline dyes by the protoplast are indicated in a recent paper by Ruhland " Die Plasmahaut als Ultra-filter bei der Kolloidaufnahme."   Ber. deut. bot. Ges., Bd., XXX, April, 1912.

IV.—Conclusion.

The composition of a particle of protoplasm is infinitely more complex than that of any other natural or artificial mass, and were scientific investigation under the academic control of some all-knowing power, no doubt man would not yet be allowed to dabble in such a difficult matter. However, as it is, we are free to break our heads over the difficulties prematurely and we progress spasmodically by a series of discoveries of isolated truths, for each of which its sponsor provides enough experimental support for our temporary acceptance of its central significance, but no sufficiently clear definition of its boundaries to enable us to piece together the fragments to form anything that can be tolerated as a picture of the whole.

It is accordingly by no means easy to correlate in any accurate way the results obtained by Czapek with those obtained by Lepeschkin, significant as either set is alone.

Certainly it is beyond question that the chemistry of the protoplast belongs to the section of microchemistry. Even were protoplasm homogeneous, the thin extension of most vegetable protoplasts would make surface-energy an important factor; but when all parts have a complex colloidal structure, biochemistry is seen to be almost entirely a matter of microchemistry in the sense of Ostwald, and the laws of adsorption will dominate the situation.

The primary difficulty we have to face is our uncertainty of exactly how far the comparatively simple principles of surface-action and micro-chemistry in a perfect fluid apply without qualification to so complicated a structure as protoplasm.

Protoplasm is certainly not a perfect fluid, for though it is incompressible and non-elastic to prolonged deformation, yet it shows some limited elasticity to brief deformation and incomplete freedom of its inner particles. Yet though it departs from a perfect fluid to this extent it is held to show the predominance of surface-tension over internal friction that marks a fluid. Rhumbler[1] has investigated the behaviour of the protoplasm of Foraminifera in this respect. When the protoplasm creeps outside its test as a naked mass and forms a new covering, the edge of the protoplasm-film always forms the same definite angle with the substratum—as judged by the inclination of the new wall to the old. This can only be brought about by surface-tension, and the angle of contact is always constant for a given species.

[1] Rhumbler. Archiv. f. Protistenkunde. Bd. I., 1902.

Granted that a protoplast is a close approximation to a true fluid, what can we say about the thickness of the surface-layer, that is the layer in which there is a special accumulation of active substances?   Will it be thin and invisible as in a perfect fluid, or does it correspond with the " Plasmahaut" for which many observers have noted a difference of appearance and which Lepeschkin finds to be less stable than the rest of the protoplast?

The Lipoids of the plasmatic membrane and selective permeability. With unusual agreement, all lines of investigation point to the presence of lipoids in the plasmatic membrane.   What may be the significance of this occurrence?   These substances are held by Overton and others to condition the selective permeability of the cell for organic substances, but the selectivity shown is from a chemical point of view quite arbitrary and, biologically, probably of no significance, though oxygen and carbon dioxide are more soluble in fats than in water.   No one has yet risen to affirm that we should regard as a biological adaptation the fact that all living cells when brought into contact with fat-solvents pass into the curious state which we call narcosis, although in these days of anæsthetic surgery, this property has become of infinite advantage to the individual.

Is it possible then that this distribution of lipoids in the cell is merely a necessary incident of the action of the Gibbs-Thomson rule upon the fats present in the cell for metabolic purposes?

The rule itself, with its thermo-dynamic basis, cannot be abrogated and the only obscurity is as to whether in so complex an organisation as that of protoplasm the emulsion particles of lipoids would be free and mobile enough to respond by the expected surface-accumulation.

It is satisfactory to find that both investigators have thrown off the incubus of Overton's theory of a continuous film of lipoid matter on the surface of the protoplast.   While Lepeschkin inclines to the view that the lipoid present is lecithin combined with the proteid, Czapek's evidence favours the view of a saturated emulsion of neutral fat.   It is true that a surface-tension of 0·68 could be obtained with the right amount of lecithin, short of saturation, but the wide uniformity of value found for so many plants makes it easier to believe in fat which has this as a limiting value and there· fore small differences of concentration would be unimportant, than to believe that exactly the right amount of lecithin is always present.

If the lipoid layer that Czapek deals with is of ultra·microscopic

thickness, then it may be that the coagulation that Lepeschkin studied does not take place in the surface-layer, but only in the underlying mass of the protoplast, and that he and Czapek are not dealing with the same structure.

Nevertheless it seems clear that substances which affect the lipoid present, either by their lower surface-tension (Czapek) or by absorption into it as narcotics (Lepeschkin) do also affect the permeation of water-soluble substances like salts and tannins. It seems therefore that there must be a close connection between the lipoid and non-lipoid material, and to this necessity the view of a chemical union seems most acceptable. How intimate the relation may be is indicated by the fact that moderate narcotic doses of ether diminish permeability to water and salts, while toxic doses of ether increase permeability, as Lepeschkin showed for *Pilobolus* exudation. The differential and variable permeability of the proto-plast for saline solutions is, however, another chapter of physiology and cannot be entered upon in this article.

SIR JOSEPH HOOKER AND CHARLES DARWIN:

The History of a Forty Years' Friendship.

By A. C. Seward.

IN 1909 the University of Cambridge celebrated the centenary of the birth of Charles Darwin and the fiftieth anniversary of the publication of the " Origin of Species." As a permanent memorial of the celebration it was decided to publish a volume of essays by British and Foreign men of science " dealing with the different aspects of Darwin's work in the light of recent contri-butions to knowledge." Sir Joseph Dalton Hooker, then in his ninety-second year, was invited to contribute an Introductory Letter to " Darwin and Modern Science." In reply to a request from the Editor for such a Prefatory note, Sir Joseph wrote, " The wish conveyed in your letter . . . that I should contribute a Prefatory note to the forthcoming Darwin Memorial volume was both gratifying and unexpected, and as an evidence of the personal consideration of the Committee of publication I feel more thankful for it than I can express. My great doubt is as to whether, in consideration of

my great age and consequent failing powers of memory and expression, I ought to undertake so grave a responsibility or occupy so prominent a position in a work of such enduring value as the memorial volume will be."

In a later letter he spoke of " more than one inchoate attempt " to write an introductory note, and added "my great difficulty is to avoid bringing myself too prominently forward, which is, however, I fear inevitable." On being asked to insert a paragraph of a more personal nature, Sir Joseph replied, " With regard to the passage which you desiderate I had one such in my original, but struck it out as merely personal if not vainglorious. I have amended and enlarged it a little." The passage is as follows:—" I may add that by no one can the perusal of the Essays be more widely appreciated than by the writer of these lines. It was my privilege for forty years to possess the intimate friendship of Charles Darwin and to be his companion during many of his working hours in Study, Laboratory, and Garden. I was the recipient of letters from him, relating mainly to the progress of his researches, the copies of which . . . cover upwards of a thousand pages of foolscap, each page containing, on an average, three hundred words." [1]

Sir Joseph was present at the Cambridge celebration in June, 1909. An American Biologist thus describes his first meeting with the Naturalist:—" My heart stood still for a moment to realize that this was Sir Joseph Hooker, the great botanist who was Darwin's friend and adviser more that fifty years ago. I had never expected to look upon his face, but there he was, ninety-two years old, yet quite able to enjoy the proceedings and converse with those who were presented to him." [2]

Since the death of Sir Joseph Hooker in December last, in his ninety-fifth year, many obituary notices have been published in which his services to science are reviewed; his friendship with Darwin, though frequently referred to, has not been treated with any degree of fulness. In the following pages an attempt is made, by quoting freely from the " Life and Letters " and from " More Letters of Charles Darwin," to give an outline sketch of a friendship which not only played an important part in determining the trend of biological thought at that time, but is a perfect example of uninterrupted confidence and affection over a period of forty years.

As a preliminary, attention is drawn to the dates of some of

[1] *Darwin and Modern Science* (Cambridge, 1909), p. 2.

[2] " The Darwin Celebration at Cambridge." By Professor T. D. A. Cockerell : *Popular Science Monthly*, January, 1910.

the more important events in the lives of the two men. Darwin was born on February 12th, 1809, at Shrewsbury; Hooker on June 30th, 1817, at Halesworth in Suffolk. Darwin died on April 19th, 1882, at Down in Kent in his seventy-fourth year, and Hooker died on December 10th, 1911, at the Camp, near Sunningdale, Berkshire. Darwin, on leaving Shrewsbury School, spent a short time as a medical student in the University of Edinburgh; in 1828 he entered Christ's College, Cambridge, proceeding to the B.A. degree in 1831. Hooker was educated at the High School and University of Glasgow, and took the M.D. degree in 1839. On December 27th, 1831, Darwin sailed in the " Beagle," returning in October, 1836. In 1839 Hooker sailed from the Medway as Assistant Naval Surgeon in the " Erebus " under Sir James Ross in his Antarctic voyage, returning in 1843. After Darwin's return home he lived for a short time at Cambridge; then in Gower Street, London, and in 1842 removed to Down—his home for the rest of his life.

The lives of the two men after 1842 afford a striking contrast. Darwin, whose health was very far from robust, devoted himself to research, living in seclusion at Down where he produced an amount and quality of work almost incredible when it is remembered to what an extent his hours of strenuous labour were relentlessly curtailed by physical disability, which to many men would have meant the complete abandonment of continuous and exacting intellectual pursuits. Hooker, on the other hand, was a man of exceptional vigour; until his retirement from the Directorship of Kew he was largely occupied with routine duties connected with Government posts. Even in his busiest official years Hooker continued to enrich botanical science by his own investigations. His first contribution to Botany was published 1837; his last in 1911. Darwin's first paper appeared in 1828 and, as in Hooker's case, the last was published in the year of his death, 1882.

In 1864 Darwin was awarded the Copley Medal, the highest scientific distinction which the Royal Society can confer: to Hooker the same honour was paid in 1887. On his ninetieth birthday Hooker received the Order of Merit.

The following brief survey serves to illustrate the activity of Sir Joseph Hooker's life up to the time of his retirement. In 1843 he was appointed assistant to the Professor of Botany in the University of Edinburgh, and in 1845 Botanist to the Geological Survey. In 1847 he sailed for India and was away three years: the account of this expedition, published under the title " Himalayan Journals,"

was dedicated to Darwin " by his affectionate friend J. D. Hooker."
In a long letter to Hooker, when he was in India, Darwin wrote in
1848, " Your letter was the very one to charm me, with all its
facts for my species' book, and truly obliged I am for so kind a
remembrance of me . . . well thank heavens, when you do come
back you will be *nolens volens* a fixture." [1] Hooker writing to Darwin
in 1854 tells him that his intention in regard to the dedication
" was formed during the Antarctic voyaye, out of love for your own
Journal . . . Short of the gratification I felt in getting the book
I know no greater than your kind, hearty acceptation of the dedica-
tion ; and had the reviewers gibbeted me, the dedication would
alone have given me real pain." [2]

In 1855 Hooker was appointed Assistant Director of the Royal
Gardens, Kew, during the Directorship of his father Sir William
Hooker, whom he succeeded as Director in 1865. In 1860 he
visited Syria ; in 1871, in company with John Ball, he travelled in
the Atlas mountains, and in 1877 made botanical explorations in
the United States with Asa Gray.

The early history of the friendship of Hooker and Darwin has
recently been retold by Professor Judd in his singularly attractive
book " The Coming of Evolution." [3] He reminds us that when
Darwin was writing his Journal of Researches he handed the proof-
sheets to Lyell who showed them to his father. The elder Lyell
passed them on to young Mr. Hooker, then in the middle of his
preparations both for an Antarctic voyage and the M.D. degree.
" So pressed for time was I," Hooker wrote in some notes supplied
to Mr. Francis Darwin when he was engaged in writing his father's
life, " that I used to sleep with the sheets of the ' Journal ' under
my pillow that I might read them between waking and rising. They
impressed me profoundly, I might say despairingly, with the variety
of acquirements, mental and physical, required in a naturalist who
should follow in Darwin's footsteps, whilst they stimulated me to
enthusiasm in the desire to travel and observe." [4] " It has been,"
Sir Joseph continued, " a permanent source of happiness to me
that I knew so much of Mr. Darwin's scientific work so many years
before that intimacy began which ripened into feelings as near to

[1] *More Letters*, Vol. I, p. 63.

[2] *M. L.*, Vol. I, p. 70.

[3] *The Coming of Evolution* (Cambridge, 1910), p. 126.

[4] *Life and Letters*, Vol. I., p. 20.

those of reverence for his life, works, and character as is reasonable and proper."

Hooker and Darwin first met in 1839 just before the departure of Sir James Ross' expedition. "My first meeting with Mr. Darwin," wrote Hooker, was in Trafalgar Square; "I was walking with an officer who had been his shipmate for a short time in the 'Beagle' seven years before, but had not, I believe, since met him. I was introduced; the interview was of course brief, and the memory of him that I carried away and still retain was that of a rather tall and rather broad-shouldered man with a slight stoop, an agreeable and animated expression when talking, beetle brows, and a hollow but mellow voice; and that his greeting of his old acquaintance was sailor-like—that is delightfully frank and cordial." [1] In 1865 Darwin concludes a letter to Hooker in these words, "Can you remember how we ever first met? It was in Park Street; but what brought us together? I have been re-reading a few old letters of yours, and my heart is very warm towards you." [2] The reference to Park Street is explained by the following extract from Sir Joseph Hooker's notes printed in the "Life and Letters":—"The next act in the drama of our lives opens with personal intercourse. This began with an invitation to breakfast with him at his brother's [Erasmus Darwin's] house in Park Street; which was shortly followed by an invitation to Down to meet a few brother naturalists. Latterly as his health became more seriously affected, I was for days and weeks the only visitor, bringing my work with me and enjoying his society as opportunity offered. It was an established rule that he every day pumped me, as he called it, for half-an-hour or so after breakfast in his study, when he first brought out a heap of slips with questions botanical, geographical, etc. for me to answer, and concluded by telling me of the progress he had made in his own work, asking my opinion on various points. I saw no more of him till about noon, when I heard his mellow ringing voice calling my name under my window—this was to join him in his daily fore-noon walk round the sand-walk."

Forty-two years after the first meeting, a year before his death, Darwin wrote, "Your letter has cheered me, and the world does not look a quarter so black as it did when I wrote before. Your friendly words are worth their weight in gold." [3]

[1] *Ibid.*, p. 19.
[2] *M. L.*, Vol. II, p. 157.
[3] *M. L.*, Vol. I., p. 39,

The correspondence between the two friends began in December, 1843, soon after Hooker's return from the Antarctic voyage. It is interesting to note that in his first letter Darwin asked Hooker to study his botanical collections from the Galapagos Islands, the Islands which exerted so strong an influence on Darwin's views in regard to species. "I was so struck," wrote Darwin to Hooker in 1844, "with the distribution of the Galapagos organisms, &c., &c., that I determined to collect blindly every sort of fact, which could bear any way on what are species." [1]   It was to Hooker that his new ideas on the origin of species were first communicated. The earlier letters contain numerous references to the immutability of species, the origin of new forms, and similar subjects. Hooker's botanical knowledge, his cautious and doubting attitude towards Darwin's as yet partially formulated views played an important part in the construction of the "Origin of Species." The frank interchange of opinions was a powerful stimulus as well as a source of pleasure to both, though it is impossible to form more than a general estimate of the influence exerted by each on the other. "Again I thank you," wrote Darwin in 1858 "for your invaluable assistance . . .   Adios, you terrible worrier of poor theorists." And later in the same year, "You may say what you like, but you will never convince me that I do not owe you ten times as much as you can owe me."   In another letter Darwin wrote, "My dear old friend, a letter from you always does me a world of good. And, the Lord have mercy on me, what a return I make." [3]

The following passages are quoted from letters written in the years preceding the publication of the "Origin." In 1844 Darwin wrote to Hooker, "but in my most sanguine moments, all I expect is that I shall be able to show even to sound Naturalists, that there are two sides to the question of the immutability of species;—that facts can be viewed and grouped under the notion of allied species having descended from common stocks." [4]   In the following year he wrote, "All of what you kindly say about my species work does not alter one iota my long self-acknowledged presumption in accumulating facts and speculating on the subject of variation, without having worked out my due share of species. . . .   I never perceived but one fault in you, and that you have grievously, *viz.*, modesty ; you form an exception to Sydney Smith's aphorism, that merit and modesty

[1] *L. and L.*, Vol. II, p. 23.

[2] *M. L.*, Vol. I, p. 105.

[3] *M. L.*, Vol. II, p. 272.

[4] *L. and L.*, Vol. II., p. 29.

have no other connection, except in their first letter." [1] In 1853 Hooker published his famous Introductory Essay to the Flora of New Zealand.   The clear statement of his position in regard to species is particularly interesting in view of the frequent interchange of ideas with Darwin during the preceding decade.   Hooker wrote, " Although in this Flora I have proceeded on the assumption that species, however they originated or were created, have been handed down to us as such, and that all the individuals of a unisexual plant have proceeded from one individual, and all of a bisexual from a single pair, I wish it to be distinctly understood that I do not put this forward intending it to be interpreted into an avowal of the adoption of a fixed or unalterable opinion on my part." [2] This section of the Essay concludes as follows :—" I cannot conclude this part of the subject better than by adopting the words of the most able of transatlantic botanists, who is no less sound as a generaliser than profound in his knowledge of details.   ' All classification and system in Natural History rest upon the fundamental idea of the original creation of certain forms which have naturally been perpetuated unchanged, or with such changes only as we may conceive or prove to have arisen from varying physical influences, accidental circumstances or from cultivation.'"   In the margin of his copy of the Essay Darwin expressed his opinion of Asa Gray's views by a single mark of exclamation. [3]

The following footnote by Hooker [4] illustrates the strong influence exerted by his friend at this period.   " Mr. Darwin not only directed my earliest studies in the subject of the distribution and variation of species, but has discussed with me all the arguments, and drawn my attention to many of the facts which I have endeavoured to illustrate in this essay.   I know of no other way in which I can acknowledge the extent of my obligation to him than by adding that I should never have taken up the subject in its present form, but for the advantages I have derived from his friendship and encouragement."   In his Address as President of the Geographical section of the British Association meeting at York in 1881, Hooker said, in reference to Geographical distribution, " As Humboldt was its

[1] *Ibid*, p. 31.

[2] Introductory Essay to The Flora of New Zealand, p. viii.   *Flora of New Zealand*, Vol. I, 1853.

[3] The library of Charles Darwin, through the kindness of Dr. Francis Darwin, is now housed in the Cambridge Botany School.   (*Catalogues of the Library of Charles Darwin*, Cambridge, 1908).

[4] Introductory Essay, p. xxii.

founder, and Forbes its reformer, so we must regard Darwin as its latest and greatest lawgiver." Three years after the publication of the Essay (in 1856), Hooker wrote, "I have finished the reading of your MS., and have been very much delighted and instructed. Your case is a most strong one, and gives me a much higher idea of change than I had previously entertained ; and though, as you know, never very stubborn about unalterability of specific type, I never felt so shaky about species before." [1] As Professor Judd pertinently remarks in a recent article in "Nature," the letters to Hooker show "how great and numerous were the 'doubts and difficulties' through which the veteran botanist battled his way towards final acceptance of his friend's views." [2]

After reading Hooker's Essay, Darwin wrote, "I have read your paper with great interest. . . . Many of your arguments appear to me very well put, and, as far as my experience goes, the candid way in which you discuss the subject is unique. The whole will be very useful to me whenever I undertake my volume, though parts take the wind very completely out of my sails; it will be all nuts to me . . . for I have for some time determined to give the arguments on *both* sides (as far as I could), instead of arguing on the mutability side alone." [3] Reverting to the Essay in another letter, Darwin wrote "In a year or two's time, when I shall be at my species book (if I do not break down), I shall gnash my teeth and abuse you for having put so many hostile facts so confoundedly well." [4] In 1854 Hooker was awarded a Royal Medal: Darwin in his congratulatory letter writes "Without you have a very much greater soul than I have (and I believe that you have), you will find the medal a pleasant stimulus ; when work goes badly, and one ruminates that all is vanity, it is pleasant to have some tangible proof that others have thought something of one's labours." [5]

Experiments on the vitality of seeds in connexion with dispersal by water or animal agency occupied much of Darwin's time. Hooker in his New Zealand Flora wrote, "I cannot think that those who, arguing for unlimited powers of migration in plants, think existing means ample for ubiquitous dispersion, sufficiently appreciate the difficulties in the way of necessary transports." [6]

Hooker preferred to regard the plants of the southern ocean as the remains of a flora which "had once spread over a large and more continuous tract of land than now exists in the ocean."

[1] *M. L.*, Vol. I, p. 437.   [2] *Nature*, November 2nd, 1911.
[3] *L. and L.*, Vol. II, p. 39.   [4] *L. and L.*, Vol. II, p. 42.
[5] *Ibid*, p. 44.   [6] Introductory Essay, p. xx.

Darwin, on the other hand, had greater faith in the possibilities of ocean transport, and was generally averse to raising and sinking continents as a means of explaining facts of distribution. " I quite agree," says Darwin in 1859 " that we only differ in *degree* about the means of dispersal ... you put in a very striking manner the mutation of our continents, and I quite agree; I only doubt about our oceans."[1] In 1854 Darwin wrote,—" When I wrote last I was going to triumph over you, for my experiment had in a slight degree succeeded; but this, with infinite baseness, I did not tell, in hopes that you would say you would eat all the plants which I could raise after immersion."[2] In a letter on the next day he added " You are a good man to confess that you expected the cress would be killed in a week, for this gives me a nice little triumph. The children at first were tremendously eager, and asked me often whether I should beat Dr. Hooker!" A few years later Darwin tells Hooker when he delivers his lecture at the British Association meeting at Nottingham (1866) to be honest and " admit how little is known on the subject of occasional means of transport."[3] In the same year Hooker wrote, " Dear old Darwin, you must not let me worry you. I am an obstinate pig, but you must not be miserable at my looking at the same thing in a different light from you."[4] In a later letter, Hooker says, " If my letters did not gêne you it is impossible that you should suppose that yours were of no use to me! I would throw up the whole thing were it not for correspondence with you, which is the only bit of silver in the affair." After expressing his opinion on continental extension and means of transport, Hooker concludes, " Oh, dear me, what a comfort it is to have a belief (sneer away)."[5] Darwin thus ends a letter to Hooker on the dispersal of seeds,—" I know all that I have said will excite in you savage comtempt towards me. Do not answer this rigmarole, but attack me to your heart's content, and to that of mine, whenever you can come here, and may it be soon."[6] In 1856 Darwin wrote,—" I thank you sincerely for all your assistance ; and whether or no my book may be wretched, you have done your best to make it less wretched ... My own mind is decided on the question of the origin of species; but, good heavens, how little that is worth."[7] In another letter, he says,—" I was particularly glad of our discussion after dinner; fighting a battle with you always clears my mind wonderfully...

[1] *L. and L.*, Vol. II, p. 144.   [2] *Ibid*, p. 54.   [3] *M. L.*, Vol. I, p. 483.
[4] *Ibid*, p. 486.   [5] *Ibid*, p. 489.   [6] *Ibid*, p. 6.
[7] *L. and L.*, Vol. II, p. 83.

The hawks behaved like gentlemen, and have cast up pellets with lots of seeds in them." [1]

The two following extracts illustrate the strength of the friendship between the two men :—" Shall you think me very impudent," writes Darwin in 1857, " if I tell you that I have sometimes thought that . . . you are a little too hard on bad observers ; that a remark made by a bad observer *cannot* be right ; an observer who deserves to be damned, you utterly damn." [2] In a later letter,—" How candidly and meekly you took my Jeremiad on your severity to second-class men. After I had sent it off, an ugly little voice asked me, once or twice, how much of my noble defence of the poor in spirit and in fact, was owing to your having not seldom smashed favourite notions of my own," [3]

In 1846 Darwin's letters contain references to the suggested preliminary publication of his views on species, which was carried into effect in 1858 on July 1st, when a joint communication from Darwin and Wallace was read before the Linnean Society. It was at the instigation of Sir Charles Lyell and Sir Joseph Hooker that Darwin on learning that Wallace "in a sudden flash of insight " had conceived the idea of Natural Selection, agreed to make public his views. A few days after the paper was read Darwin wrote to Hooker,—" If you see Lyell, will you tell him how very grateful I feel for his kind interest in this affair of mine. You must know that I look at it as very important for the reception of the view of species not being immutable, the fact of the greatest geologist and botanist in England taking *any sort of interest* in the subject. I am sure it will do much to break down prejudices." [4] An address by Sir Joseph Hooker at the Darwin-Wallace celebration on July 1st in 1906, by the Linnean Society, concludes with these words,— " It remains for me to ask for your forgiveness for intruding upon your time and attention with the half-century old, real or fancied memories of a nonagenarian as contributions to the history of the most notable event in the Annals of Biology that followed the appearance in 1735 of the " Systema Naturæ " of Linnæus." [5]

Writing to Wallace in 1859 Darwin says,—" Dr. Hooker has become almost as heterodox as you or I, and I look at Hooker as *by far* the most capable judge in Europe." To the same friend Darwin wrote,—" Hooker is publishing a grand Introduction to the Flora of Australia, and goes the whole length." [6]

¹ *Ibid*, p. 85.   ² *Ibid*, p. 92.   ³ *Ibid*, p. 96.   ⁴ *Ibid*, p. 127.
⁵ The Darwin-Wallace Celebration (London, 1908), p. 16.
⁶ *L. and L.*, Vol. II, pp. 146, 163.

To Hooker, after the publication of the Essay, Darwin wrote,
—" I have finished your Essay... To my judgment it is by far
the grandest and most interesting essay, on subjects of the nature
discussed, I have ever read." After some criticism, he concludes,
—" But I am an impudent dog, one must defend one's fancy
theories against such cruel men as you. I dare say this letter
will appear very conceited, but one must form an opinion on what
one reads with attention and in simple truth, I cannot find words
strong enough to express my admiration of your Essay, My dear
dear old friend, yours affectionately, C. Darwin." [1]

In the concluding paragraph of this Essay, Hooker writes,—
" I would further observe here, to avoid ambiguity, that my friend,
Mr. Darwin's, just completed work (1859) " On the Origin of
Species by Natural Selection," from the perusal of much of which
in MS. I have profited so largely, had not appeared during the
printing of this Essay, or I should have largely quoted it." [2]

On the publication of the " Origin " Hooker wrote,—" I am a
sinner not to have written you ere this, if only to thank you for
your glorious book—what a mass of close reasoning on curious
facts and fresh phenomena—it is capitally written and will be very
successful.... Lyell, with whom we are staying, is perfectly
enchanted, and is absolutely gloating over it. I must accept your
compliment to me, and ackowledgment of supposed assistance
from me, as the warm tribute of affection from an honest (though
deluded) man, and furthermore accept it as very pleasing to my
vanity ; but my dear fellow, neither my name nor my judgment
nor my assistance, deserved any such compliments, and if I am
dishonest enough to be pleased with what I don't deserve, it must
just pass." [3] In reply Darwin wrote,—" I cannot help it, I must
thank you for your affectionate and most kind note. My head
will be turned. By Jove, I must try and get a bit modest....
You have cockered me up to that extent, that I now feel that I can
face a score of savage reviewers." [4] In another letter he added,—
" Your approval of my book, for many reasons, gives me intense
satisfaction ; but I must make some allowance for your kindness
and sympathy. Anyone with ordinary faculties, if he had *patience*
enough and plenty of time, could have written my book." [5]

In 1860 Hooker visited Syria. Darwin thus refers to the

[1] *L. and L.*, Vol. II, p. 259.
[2] Introductory Essay to the Flora of Tasmania, p. cxxviii.
(*Flora of Tasmania*, Vol. I, 1859).
[3] *L and L.*, Vol. II, p. 222.   [4] *Ibid*, p. 228.   [5] *Ibid*, p. 243,

proposed expedition,—" I am astonished at your news.... I am become such an old fogey that I am amazed at your spirit. For God's sake do not go and get your throat cut. Bless my soul, I think you must be a little insane. How I shall miss you, my best and kindest of friends. God bless you." [1]

In 1881, the year before his death, Darwin wrote to Hooker,— " For Heaven's sake never speak of boring me, as it would be the greatest pleasure to aid you in the slightest degree." [2] The letter deals with several points raised by Hooker connected with the approaching address to the Geographical Section of the British Association at York. From first to last throughout a period of over forty years, Hooker and Darwin were in constant and intimate correspondence : the opinions and facts contained in Darwin's letters, and in the few from Hooker which have so far been published, are of great scientific value : but, after all, it is the intense human interest of the unbroken and progressive friendship that leaves the most lasting impression.

[1] *Ibid*, p. 337.　　　[2] *L. and L.*, Vol. III, p. 246.

NOTES ON RECENT LITERATURE.

Modern Systems of Classification of the Angiosperms.

Handbuch der Systematischen Botanik. Von Dr. Richard R. v. Wettstein. Zweite, umgearbeitete Auflage. Mit 3692 Figuren in 600 Abbildungen und mit einer Farbentafel. Leipzig und Wien. Franz Deuticke. 1911.

Vorträge über Botanische Stammesgeschichte. Ein Lehrbuch der Pflanzensystematik. Von J. P. Lotsy. Dritter Band : Cormophyta Siphonogamia, erster Teil. Mit 661 Abbildungen im Text. Jena. Gustav Fischer. 1911.

Föplanterne (Spermatofyter). Med 591 i texsten trykte Figurer eller Figur-grupper. Af Dr. Eug. Warming. Köbenhavn og Kristiania. 1912.

IN these three volumes, published almost synchronously, we have the views of three leading botanists of different nationalities on the classification of the plants.

Wettstein's[1] is a sumptuous volume dealing with the whole vegetable kingdom : Warming's deals with the Gymnospermæ and Angiospermæ principally, with an introductory chapter of nearly seventy pages giving a comparative account of the life-history of the Bryophyta and Pteridophyta : Lotsy's is the third volume of his well-known work, the first 440 pages being devoted to the Gymnospermæ, and the second 510 to the earlier orders of the Angiospermæ. In the present notice, only the portions of the above works which deal with the Angiospermæ are discussed.

None of the three authors accepts wholly the system of classi-

[1] The first edition was published in 1907.

fication by Engler; but each is very much nearer to this system than it is to that of de Candolle as still used in France or that modification of de Candolle's system by Bentham and Hooker adopted in the British Empire. Practically all countries except France and England have adopted some system which is based on that of Eichler; and it is therefore one of the little ironies of history that the beginnings of this last system are to be traced to the writings of the English botanist, Lindley, and the French botanist, Brongniart.

In the arrangement of Dicotyledons and Monocotyledons, both Wettstein and Warming begin with the orders having simpler and indefinite flowers, and follow with the orders having more complex and definite flowers. Discussing the question of the more primitive type of flower among living Angiospermæ, Warming (p. 49) regards the acyclic types as " undoubtedly on the whole older; and the number of their leaves is large and uncertain. On the contrary, the cyclic arrangement in which a smaller and definite number of parts occurs is a younger stage."

The three books furnish three different views with regard to the relationships of the Dicotyledons and Monocotyledons. Warming follows Engler in placing the Monocotyledons first, but states (p. 84) that " in what developmental relationship these two classes stand to one another and from whence they took their origin is uncertain. Some consider the Monocotyledons as a younger type which has descended from the older Dicotyledons, others *vice versa*. It is best, at any rate for the present, to place them as two equally independent lines parallel with one another." Wettstein definitely looks upon the Monocotyledons as a monophyletic group which has sprung from the Polycarpicæ (or Ranales). Both Wettstein and Warming place the Helobiæ first among Monocotyledonous orders; and Warming arranges these orders as follows :—Helobiales, Glumales, Pandanales, Palmales, Arales, Enantioblastæ, Liliales, Orchidales, Scitaminales. The chief differences in this arrangement and the one adopted by Warming in his earlier work[1] are seen in the sub-dividing of the older Spadiciflorae into three orders, Pandanales, Palmales, and Arales, and in the placing of the Scitaminales instead of the Orchidales at the head of the class. Wettstein retains the order Spadiciflorae, and even places it at the head of the Mono-cotyledons, his arrangement being as follows :—Helobiæ, Liliiflorae, Enantioblastæ, Glumiflorae, Cyperales, Scitamineæ, Gynandræ, Spadiciflorae. Lotsy treats the Monocotyledons as a diphyletic group. He derives them all from Dicotyledonous ancestors; and this indeed may be regarded as the present prevailing view, owing largely to Miss Sargant's convincing statement of the case.[2] In Lotsy's treatment, the Spadicifloral families—Araceæ, Lemnaceæ, Cyclanthaceæ, Palmaceæ, Pandanaceæ, Sparganiaceæ, and Typha-ceæ—follow the Piperales, a view which has received support in several quarters in recent years. The remaining Monocotyledons are placed by Lotsy after the Ranales; and his arrangement of these Monocotyledons follows that by Wettstein.

Warming maintains his earlier view as to the position of the Juncaceæ in the Glumales. In most arrangements, this family is

[1] See " A Handbook of Systematic Botany " by E. Warming, translated and edited by M. C. Potter; 1895.
[2] See *Ann. Bot.*, XXII, p. 121 ; 1908 (and literature cited).

placed in the Liliifl[oe]ræ. Warming states (p. 102) that "the Juncaceæ may be placed first [among the Glumales] as they represent the typical trimerous flower [of the Monocotyledons] and have a capsular fruit"; and he traces an evolutionary sequence from the Juncaceæ through trimerous genera like *Cyperus, Scirpus,* and *Eriophorum* to the more specialised genus *Carex.* Similarly, in the case of the Gramineæ, the trimerous *Bambusa,* through genera like *Oryza,* connects the Juncaceæ with the specialised *Anthoxanthum,* etc.

Wettstein's view that the Helobiæ have given rise to the remaining orders of Monocotyledons does not appeal to us as being very convincing. We prefer, in this case, the view adopted by Lotsy that the Helobiæ are an unsuccessful group in so far as they have probably given rise to no higher forms; and this also is the view adopted by Rendle.[1]

There seems, on the whole, to be a considerable amount of agreement among botanists that the Monocotyledons have been derived from the Dicotyledons; and, although the former do not attain the high vegetative and anatomical development seen in many of the latter, it seems right that the Monocotyledons should be placed after the Dicotyledons. It is not, however, to be expected that systematists will at present go to Lotsy's extreme of dividing the Monocotyledons into two groups and placing these in different places among the Dicotyledons. In the distant future, it is possible that the Monocotyledons will disappear as a separate group; but much work remains to be done before such a drastic view can be adopted in systematic works, which rightly lag behind and act as a check upon the speculations of morphologists.

One result of the prevailing view of the origin of the Monocotyledons from the Dicotyledons is that attention is now concentrated on the latter group in the attempt to solve the problem of the origin of the Angiospermæ. Lotsy discusses this question, but admits that he has no solution to offer. It is therefore most singular that his arrangement of the Dicotyledons—only the earlier parts of which appear in the present volume—should be on lines which assume that the problem has been settled, and settled in a definite manner. Lotsy has evidently no scruples such as we expressed in the concluding lines of the last paragraph: he seems, on the contrary, to regard his arrangement of orders as a spur to apply to morphologists to hasten the settlement of difficult and intricate problems. However, it is impossible to criticise Lotsy's views of the Dicotyledons until his fourth and last volume has appeared.

Both Warming and Wettstein recognise two sub-classes of Dicotyledons, the Choripetalæ and the Sympetalæ. The former, of course, are the Archichlamydeæ of Engler; and Wettstein subdivides the Choripetalæ into the Monochlamydeæ (beginning with Verticillatæ and ending with Centrospermæ) and the Dialypetalæ (beginning with Polycarpicæ and ending with Umbelliflorae). Neither Warming nor Engler adopts the latter sub-division. However, there is agreement by Warming, Engler, and Wettstein in placing first those monochlamydeous forms which have no obviously near relatives with dichlamydeous perianths.

Whilst fully agreeing with the principle of this arrangement,

[1] "The Classification of Flowering Plants": vol. I; 1904.

we venture to differ on a point of detail from all three of the authorities named. We refer to the position accorded to the order Verticillatæ. It will be remembered that *Casuarina*—the only genus of the order—was regarded by Eichler[1] as probably best placed in his order Amentaceæ; and it was once so placed by Engler[2] himself. It was removed from this position after the account by Treub[3] of the processes that went on in the ovule; and it is now usual (though, we believe, quite erroneous) to place the Verticillatæ as the first, and presumably the most primitive order of Dicotyledons. Warming justifies this position of the order is the following words (p. 167):—" By the transfusion tissue, by the type of stomata, and especially the ovular peculiarities, this order seems to be related with the Gymnospermæ, especially the Gnetales." The ovular peculiarities are thus summarised:—" In the nucellus, which has two integuments, many embryo-sacs are formed, of which only one is fertilised. The egg-apparatus consists, as among Angiosperms, of an egg-cell and two synergidæ; but antipodal cells are not formed. Before fertilisation, a prothallus of many free nuclei is formed, which after fertilisation becomes a nutritive tissue. The fertilisation is chalazogamic." These remarks are based on the work of Treub (*loc. cit.*). Treub's observations, however, have been shown by Frye[4] to be inaccurate in a few particulars, such as the possession of an anomalous embryo-sac. All the other characters described by Treub as occurring in *Casuarina* have been found in *Carpinus*, and many of them in *Corylus*, *Betula*, and *Alnus*. The characters here referred to are the occurrence of chalazogamy, the occurrence of more than one embryo-sac (numerous embryo-sacs occurring in *Carpinus*), the formation of a cæcum from the originally isodiametrical embryo-sac, the occurrence of tracheids among the embryo-sacs, the entry of the pollen-tube at the base of the cæcum in *Corylus* and *Carpinus*, the closure of the micropyle, and the fusion of the ovule with the wall of the ovary. It has also been shown[5] that in the type of inflorescence, regarded as a modification of Eichler's type-diagram of the group, the cone-like structure of the amentum is not unlike that of *Alnus*; and the bacterial tubercles on the roots of both genera may be instanced as a common biological feature. The typical Angiospermous embryo-sac observed by Frye (*loc. cit.*) and the carpellary investment round the ovule described by Treub show that the genus should not be separated from the Angiosperms, as Treub suggested it should be; and the results obtained by Benson (*loc. cit.*) prove decisively that the position accorded to *Casuarina* by Eichler was a very reasonable one. There remain the vegetative characters of *Casuarina*—the switch-like habit, the specialised phyllotaxy, the transfusion tissue, and the type of stomata—to consider; and we suggest that these are merely biological adaptations to the dry climate which species of *Casuarina* affect. On this view, the points of real similarity between *Casuarina*

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[1] " Syllabus der Vorlesungen " ; 5 Auflage ; 1890.

[2] " Pflanzenfamilien," III, Pt. I, p. 16 ; 1889.

[3] *Ann. Jard. Bot. Buitenz.*, X, p. 145 ; 1891.

[4] *Bot. Gaz.*, XXXVI, p. 101 ; 1903.

[5] See especially Benson, Sanday, and Berridge : " Contributions to the Embryology of the Amentiferæ : Part II, *Carpinus Betulus* " ; in *Trans. Linn. Soc.*, VII, Pt. 3, 1906.

and *Ephedra,* upon which both Wettstein and Warming lay stress, have no more taxonomic significance than the presence of root-tubers in *Cycas, Myrica, Alnus,* etc.; and the direct relationship of Angiosperms and Gymnosperms in general, and of *Ephedra* and *Casuarina* in particular, is a view which cannot be upheld. It may be that systematists will not be disposed to reduce the Verticillatæ to tribal rank, equivalent with the Coryleæ and Betuleæ, as Benson at first suggested; but that her work vindicates the position accorded to *Casuarina* by Eichler admits, in our judgment, of little or no doubt.

In fact, we have the most serious doubts as to whether any of the modern speculations which attempt to derive directly the Angiospermæ from the Gymnospermæ have any permanent value; and hence we are not disposed to take very seriously some of the phylogenetic tables given by Lotsy. In one of the latter (see p. 442), a hypothetical group—Drimytomagnolieæ—is directly derived from the Bennettiteæ. This supposition, in our opinion, places too much weight on a hypothesis of the so-called flower of the Bennettiteæ, and too much weight on the very isolated phenomenon of the simple anatomy, seen in only a single tribe of the Magnoliaceæ. Whatever view be taken of the simple wood of the Drimydeæ, its phylo-genetic value is greatly discounted by the fact that normal Angiospermous wood occurs in tne remaining tribes of the family.

Generally, we believe that the Angiospermæ and Gymnospermæ are connected only by some ancient and unknown ancestors which gave rise on the one hand to the more primitive Gymnospermæ, and on the other hand to some unknown group of primitive Angiospermæ. On this view, the union of the Gymnospermæ and Angiospermæ by Engler and others into a single division (Abteilung) —Embryophyta Siphonogama—is not very useful, as it tends to obscure the real relationships of the two sub-divisions.

Warming's treatment of the Centrospermæ, a name which he now adopts in place of Curvembryæ which he formerly used, differs essentially from that accorded to the order by Engler. Wettstein, who adopts with little modification the sequence of families given by Engler, begins with the simple and presumably primitive Chenopodiaceæ and goes on to the more complex and presumably derived Aïzoaceæ and Caryophyllaceæ. Warming (p. 200) states that, with regard to the families of the order, "it is uncertain what genetic relationships they bear to one another, and in what sequence they with most justice should be placed. Some authors begin with the incomplete types, and then take the more highly differentiated ones which possess both calyx and corolla, split stamens, epigyny, etc. Here, for the sake of convenience ("af praktiske Grunde,") the Caryophyllaceæ are placed first. After them are taken the simpler, formally reduced types which are considered to be most directly derived from them. After these, follow others with a single perianth. Lastly, families with epigyny and numerous stamens formed by division are taken." Danish botanists who have become accustomed to the arrangement of the Centrospermæ in Warming's former work will doubtless appreciate these "praktiske Grunde"; and doubtless the more conservative among them will even enter a more or less mild protest against the change of name from the (to them) familiar Curvembryæ to the (to them) unfamiliar Centrospermæ; but those of us who are constitutionally inclined to regard systematic

botany as belonging to the realm of philosophical science, and not as a complex of pigeon-holes for the docketing of plants, will be disposed to resent the too-frequent intrusion of mere "praktiske Grunde" into a department of science. It seems to us that Engler's arrangement of the Centrospermæ is a very logical one; and the only complaint we have to make with regard to it is that we would prefer to look upon the group as a complex of orders, and to elevate to the rank of orders the four sub-orders which, according to Engler, constitute the whole group. There are fewer difficulties in regarding the Chenopodiaceæ as the most primitive of the Centrospermæ than in regarding the Caryophyllaceæ in that light. There are so many points of specialisation in the Caryophyllaceæ—the straight ovary of *Dianthus*, for example—that it seems reasonable to regard the family as a whole as having sprung from one in which those specialised characters are absent ; and with regard to the Aïzoaceæ, including *Mesembryanthemum*, the whole flower is so extremely specialised in all its parts, that no one, we presume, would dream of regarding its numerous stamens, carpels and ovules as primitive.

The position of the Cactaceæ has long been a matter of controversy among systematists ; and the family has been placed in many different positions by different botanists. Both Wettstein and Warming place it immediately after the Aïzoaceæ, though Wettstein regards it as coming within the limits of the order Centrospermæ, whilst Warming places it in a separate, but allied, order, the Cactales. Thus both these authorities differ with Engler who places it immediately after his Parietales. There was some discussion on the Cactaceæ in this Journal a little time ago. The discussion involved a consideration of the systematic position of the Cactaceæ ; and Mrs. Arber[1] stated that she was inclined to think it "a justifiable hypothesis" that the Cactaceæ are derived from the same stock as the Nymphæaceæ. In Wettstein's arrangement, Mrs. Arber's view receives no support ; for although the Cactaceæ are here (to quote Mrs. Arber) "placed immediately before the Polycarpicæ," there is no implied connection ; but rather the reverse. The Cactaceæ, according to Wettstein, are the last and most specialised of his Monochlamydeæ ; and the Polycarpicæ are the first and least specialized of his Dialypetalæ. It is not natural to derive the lowest members of one group from the most specialised members of another ; and as a matter of fact Wettstein connects his Polycarpicæ with the Hamamelidales which he places in his Monochlamydeæ. On the the other hand, although the Opuntiales (with the single family Cactaceæ), are placed apparently high up among Engler's orders, yet a study of his major divisions, which are unfortunately not named and thus elude the attention of non-systematists, leaves it possible to regard the Parietales and the Opuntiales together as having sprung from Ranalian ancestors ; and thus the feature which Mrs. Arber (*loc. cit.*) points out as being common to the Ranales and the Opuntiales are much more easily explicable on Engler's view of the relationships of these families than on Wettstein's and Warming's.

Incidentally, it may be worth while emphasising here that there are several cases where Engler has been misunderstood by British

[1] *New Phytologist*, IX, p. 333, 1910 (see also de Fraine, in *Ann. Bot.*, XXIV, p. 125, 1910).

botanists, owing to their having failed to notice the subtlety and significance of his numerous and often unnamed major divisions, divisions we mean of higher than ordinal rank.

Readers of this Journal, who are familiar with Mr. Wernham's articles on Sympetalæ, will naturally wonder how this group is treated by Wettstein and Warming. Warming states (p. 346) that "the Sympetalæ form the last, highest developed and presumably the youngest sub-class of Dicytoledons. On the whole, they seem to form quite a natural group; but they scarcely form a phylogenetic line; and the future will undoubtedly unite certain classes with polypetalous ones." Then follows Warming's arrangement into eleven orders beginning with the Bicornes (Engler's Ericales) and ending with the Synandræ (Engler's Campanulatæ), an arrangement which differs only in slight respects from Warming's earlier one. The orders are arranged in two major groups (p. 348). "First come those with two whorls of stamens (pentacyclic), pre-sumably the oldest type. ...... Then follow the Tetracyclicæ which are sub-divided into hypogynous forms and epigynous forms." Warming (p. 49) holds that "On the whole, symphylly ('Sambladethed') points to a younger and probably a more perfect stage of development *in any given circle of affinities* [italics ours]. Symphyllous organs, *e.g.*, symphyllous corollas or sym-phyllous gynœcia are laid down as polyphyllous ones;" and here fig. 72 (after Payer) is cited, showing that in the development of the flower of *Borago*, the organs which later are coherent, are at first free. Warming admits (p. 356) that the present position of the Primulales among the other sympetalous orders is not clear, chiefly on the ground of the presence of two integuments in the ovule of the Primulales, and "possibly they are connected with some choripetalous type." We ourselves are prepared to state this case more strongly, and to argue for a position of the Primulales close to that of the Centrospermæ. Wettstein agrees in deriving the Plumbaginaceæ from the Centrospermæ; but he strangely allies the Primulaceæ with the Bicornes, and derives both these groups from his Guttiferales (including Dilleniaceæ and *Hypericum*).

Wettstein boldly admits that the Sympetalæ are polyphyletic, and derives almost every sympetalous order from different Dialy-petalous ancestors.

Lotsy's work has not yet reached the Sympetalæ; but as the case for the polyphyletic origin of the Sympetalæ is much stronger than for that of the Monocotyledons, we may safely predict some interesting suggestions when Lotsy's final volume appears.

One other point in Warming's book deserves notice. The orders and families recognised by him are smaller, and in our judgment more practicable than those recognised by Engler. For example, Warming's Geraniales are practically the same as Engler's sub-order Geraniineæ; and the immense size of some of Engler's orders, *e.g.*, his Geraniales (which include the Euphorbiaceæ and even the Callitrichaceæ) make them almost if not quite unworkable. Again, Warming sub-divides Engler's family Rosaceæ, into four really workable families, the Rosaceæ (*sensu stricto*), Amygdalaceæ, Chrysobalanaceæ, and Pomaceæ; and it cannot be successfully maintained that the family Rosaceæ as ordinarily understood is botanically comparable with such families as are ordinarily held to comprise the Liliiflorae.

Perhaps it will not be inopportune to conclude this notice with a reference to a personal matter.

One of the most important preliminary points which have had to be decided in connection with the publication of the *Cambridge British Flora* has been whether or not the arrangement of the families adopted by Bentham and Hooker should be retained.   In favour of retaining this arrangement is the fact that it is the one in current use by botanists in all parts of the British dominions; and an arrangement which is so widely used cannot lightly be set aside. On the other hand, it has to be admitted that in almost all other countries, some other arrangement is in use.   The arrangement in current use by French botanists is that of de Candolle, upon which Bentham's and Hooker's was based; and the two systems are so closely related, that they may, for the present purpose, be considered the same; but in Germany, Switzerland, Norway, Sweden, the United States of America, and in several other countries, the newer floras are either based on Engler's arrangement, or are on some plan, which, for the present purpose, may be regarded as nearly identical with it.   What really had to be decided therefore was whether the Candollean system, used by French and British botanists, or the Englerian system, used by nearly all other botanists, should be adopted.   Two other possibilities were seriously suggested : one was to follow the system of Bessey,[1] and the other was to modify Bentham's and Hooker's system in accordance with some modern views.

After carefully considering the whole matter, it was decided to adopt Engler's arrangement, for the reason that it is the system most in accord with modern views of plant affinities, and, at the same time, a system which is used by a large number of botanists of many nationalities.   It is also accessible to botanists in the volumes of the *Pfamzenfamilien*, where the details of the whole system have been elaborated.   The leading British systematists were consulted on the matter; and they agreed that there was really no serious alternative to this plan.   The way was finally cleared when it appeared that the late Sir J. D. Hooker, before his death, was prepared for the change.   The disadvantages incident to all changes will naturally be felt for some time by British botanists ; but in the end it will be a solid gain to have a British flora arranged in such a way that it can be easily compared with the great majority of the best floras of newer and other countries.

It is not, of course, possible to undertake to adopt every detail of Engler's arrangement : the right to modify details, as may be considered advisable, must be reserved.   C.E.M.

MEIOSIS AND ALTERNATION OF GENERATIONS.

THE demonstration by Lloyd Williams (1904) in *Dictyota* and by Yamanouchi (1906) in *Polysiphonia* that the free-living tetraspore-bearing plants are characterised by diploid nuclei, so that they could be regarded as cytologically equivalent to the "sporophyte" of the archegoniates, *i.e.*, to the diploid phase of the life-cycle at the end of which meiosis occurs, marked an important epoch in the development of our knowledge of the relation of meiosis to alternation

[1] See *Bot. Gaz.*, XXIV, p. 145, 1897.

of generations.   Previously to these discoveries there had been a tendency to regard the carpospore-bearing (*i.e.*, the immediately post-zygotal) phase of the life-history of Florideæ as the equivalent of the " sporophyte " of archegoniates and more particularly as the equivalent of the sporogonium or fruit-body of the Bryophytes.   By the upset of that comparison, so far as the cytological correspondence of carpospores and archegoniate spores was concerned, the value of certain evidence for the theory of the antithetic origin of alternation of generations in the Pteridophyta was *pro tanto* weakened, though, as has often been pointed out, that theory cannot be *disproved* by any evidence of this class.

The recently published results of Svedelius on *Delesseria* and of Lewis on *Griffithsia, Polysiphonia* and *Dasya*, entirely confirm those of the previous workers and suggest that the diploid character of the tetrasporic individuals of Florideæ, correlated with meiosis at formation of the tetraspores, is quite general.

Svedelius (1911) shows that the nuclei of the tetrasporic plants of *Delesseria sanguinea* have the diploid number of chromosomes (40), while the sexual (demonstrated only in the female) plants have the haploid number (20), as have the tetraspores themselves, the formation of tetraspores showing the typical phenomena of tetrad or reduction-division, with synapsis, and a heterotypic followed by a homotypic division.

Lewis (1909) showed in *Griffithsia* that the zygote nucleus, the carpospore nuclei and the nuclei of tetrasporic plants all contain 14 chromosomes, while at the first division of the nucleus of the tetraspore mother-cells the number of chromosomes is reduced to one-half, each tetraspore nucleus containing 7 chromosomes.

In a later paper the same author (1912) shows by means of cultural experiments in which the plants were allowed to develop in the open sea that the carpospores of *Polysiphonia violacea* produce tetrasporic plants only, while the tetraspores of *Griffithsia Bornetiana* and *Dasya elegans* produce sexual plants only.

Thus the occurrence of a regular alternation of tetrasporic with sexual plants, the diploid nature of the nuclei of the former, and the occurrence of meiosis at the production of tetraspores is now established on a much broader basis.

Now since, as Lewis remarks (1909, p. 682), " the intercalation by amplification of an *unlike* phase seems to be the very pith of the theory of antithetic alternation," the establishment of this fact, that the cytological alternation takes place not between the independent vegetative plant and the carpospore-bearing fruit-body, but between the sexual plant and the tetrasporic plant *plus* the immediately preceding carposporic phase, introduces a new complexity into the attempted comparison with the Archegoniates.   In the case of *Dictyota*, where there is no carposporic phase in the life-history, a direct comparison obviously suggests a homologous origin of the phenomenon of alternation, since the two cytologically differing generations are vegetatively alike and it is gratuitous to suppose that one of the two has been " intercalated " in the life-history. It is much simpler to regard the two generations as homologous by descent, the production of the two kinds of reproductive cells having been originally, as in the lower Algæ, entirely under the control of external conditions, and having now become localised in the two

alternating generations, meiosis occurring at tetraspore formation, the second great break in vegetative development, and thus a rhythmic life-cycle with two alternate, cytologically differentiated but vegetatively identical, phases being established.

But the case of the Florideæ with a carposporic phase is not so simple. Here we have not only the tetrasporic plant, but the immediately preceding carposporic phase, exhibiting the diploid condition, so that the carpospores, while they mark a vegetative break do not mark a cytological break in development. For this reason Svedelius (1911, p. 317) suggests that they should be called *carpogonidia*, and for this reason also Yamanouchi considers that the carposporic phase should be considered as *part of the sporophyte generation, which is continued as the tetrasporic plant.* He considers that " the tetrasporic plant may have arisen by a suppression of the reduction phenomena in connection with the carpospore, so that it germinates with the sporophytic number of chromosomes, producing a plant with this number, which consequently becomes at once a part of the sporophytic phase. The period of chromosome reduction would be thus postponed from the carpospore to a later period in connection with the newly formed plant" (1906, p. 435). The resemblance of the tetrasporic to the sexual plant Yamanouchi explains by the similar environmental conditions under which they develop.

According to this view we can construct a series, starting with forms like some of the lower Algæ in which meiosis occurs at germination of the zygote (Karsten, *Spirogyra* : Klebahn, Desmids). From such forms the ancestors of the Florideæ were developed, the carposporic phase being intercalated between the zygote and the beginning of the next free-living generation, and this intercalated phase was characterised by the possession of diploid nuclei, meiosis occurring at carpospore formation. This is supposed to be supported by the case of *Nemalion*, in which plant Wolfe concluded, though he did not rigorously demonstrate, that meiosis occurred at carpospore formation. Tetraspore formation is absent in this and in some other genera of Florideæ, and the (supposed) haploid carpospore might be expected to give rise to a sexual haploid plant. Finally we have the Florideæ, with tetraspores as well as carpospores, in which, according to Yamanouchi, meiosis has been deferred from carpospore formation to tetraspore formation so that the tetrasporic plant retains the diploid character of the " sporophyte " generation.

This ingenious theory of Yamanouchi's, while explaining the state of affairs in the higher Florideæ, does not fit in well with the case of *Dictyota*, in which there are no carpospores, and in which it is quite gratuitous and *a priori* improbable to consider the tetrasporic generation as antithetic. Further we have no evidence, beyond the existence of forms with carpospores but no tetraspores, that the tetrasporic generation in the higher Florideæ arose in evolution *subsequently* to the carposporic phase, nor is there any obvious reason why meiosis should have been deferred in the way supposed. Taking *Dictyota* and the Florideæ together we have three types of life-history in which something more than the sexual plant is involved; sexual plant *plus* tetrasporic plant, sexual plant *plus* carposporic phase, and sexual plant *plus* carposporic phase *plus* tetrasporic plant. It seems more legitimate, therefore, to consider the tetrasporic plant and the carposporic phase separately, rather

than as connected phenomena. If we take this view it is natural to suppose that the tetrasporic plant is essentially homologous with the sexual plant, while the carposporic phase has been intercalated, and is antithetic in the original sense of Celakovsky and Bower, which has no reference to the position of meiosis. This is substantially the view taken by Lewis (1909).

There is now abundant evidence that meiosis does not occur at corresponding points in the life-history throughout the plant-kingdom. All we can say is that it has to occur *at some point* between successive zygoses, and that it always occurs *at some break* in the continuity of vegetative development. Assuming that it originally occurred on germination of the zygote, and was thus intimately associated with *the only break of the kind* occurring in plants with a simple life-history, it has been shifted, in plants with a more complex but regularly periodic life-history, to some other point, which varies in different cases, but is generally coincident with obligate spore-formation. If this be so it is a mistake to insist on recognising a " sporophyte " which is cytologically characterised and is identical throughout the different phyla, showing meiosis at spore-formation, and it follows that neither the homologous nor the antithetic origin of such a sporophyte can be predicated as a universally valid theory.

We have to recognise two main types of evolution of spore-bearing phases of the life-history. First the evolution of a post-zygotal fruit-body producing spores (*Coleochæte*, Florideæ, Bryophyta), secondly, the appearance of a free-living spore-bearing alternate generation (*Dictyota*, Florideæ, Pteridophyta). These two phenomena are quite distinct, and may or may not co-exist. Meiosis may occur at the formation of the spores of either the first (Bryophyta) or of the second (*Dictyota*, Pteridophyta) or of neither (*Coleochæte*). It seems better to confine the term *sporophyte* (=spore-bearing *plant*) to the latter type of phase, and to use some such term as *post-zygotal sporophase* for the former. The natural interpretation of their origin is that the " sporophyte " in this sense is homologous with the sexual plant and that the post-zygotal sporophase is antithetic, if it be desired to retain that term for an unlike intercalated phase in the life-history. It requires much stronger evidence than has ever been brought forward to justify an acceptance of the view that these two phases have any direct connexion in evolution.

A.G.T.

LITERATURE.

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FLORAL EVOLUTION : WITH PARTICULAR REFERENCE

TO THE SYMPETALOUS DICOTYLEDONS.

By H. F. WERNHAM.

VII. INFERÆ : PART I. RUBIALES.

THE significance accorded to the relative position of the gynæcium in the flower as a critical classificatory character was much greater formerly than it is at the present time.   In Lindley's system, for example, the character of sympetaly is entirely subordinated to that of epigyny, and this author criticizes forcibly the primary divisions of the Dicotyledons made by Jussieu, based on the nature of the perianth and the cohesion of its parts.

We have discussed already in our earlier chapters the significance of epigyny, and the attempt has been made to portray the biological advantage accruing from this character.   We shall learn in the sequel that those forms which are universally regarded as standing in the van of floral evolution invariably possess an inferior ovary ; and the Inferæ,[2] which form the subject of this and the following chapters, include some 20,000 species, or, roughly speaking, more than one half of the total number of species in Sympetalæ.   We shall see, moreover, that these species are divisible into a few very natural groups, which display in their turn unmistakeable signs of mutual affinity, exclusive of the epigynous character ; while their connection with the other sections of Sympetalæ—Heteromeræ and Bicarpellatæ of Bentham and Hooker—must needs be traced only through a very remote archichlamydeous ancestry.   The problem of the origin of the Inferæ, in fact, will afford us yet another illustration of the

[1] See Lindley : *The Vegetable Kingdom*.   Third Edition, pp. 243-246.

[2] The collective name given by Bentham and Hooker to Rubiales, Asterales, and Campanales (see table, p. 219) all characterized by epigyny.

polyphyletic origin of the Sympetalæ ; this aspect will appear in the sequel, where the importance of epigyny as a critical character —in the delimitation of the larger groups at any rate—will become apparent.

We must first deal in some detail with the groups concerned. Particulars of the division into cohorts and families according to both the modern systems, together with the significant floral characters of each family, are shewn in the accompanying table ; the actual order of the families has been altered for the sake of convenience in displaying the comparison between the two systems.

Perhaps the most striking feature of this comparison is the essential difference between the two systems in the primary allotment of the families into cohorts (natural orders). This difference, broadly speaking, is three-fold, having regard to 1st, the inclusion of Cucurbitaceæ in Engler's Sympetalæ ; 2nd, the association of Compositæ and Campanulaceæ in the same cohort by Engler and their separation into different cohorts by Bentham and Hooker ; 3rd, the separation of Compositæ from the Valerianaceæ –Dipsacaceæ group into different cohorts by Engler, and their inclusion in the same cohort by Bentham and Hooker. These differences reflect the relative stress laid on different biological tendencies by the respective authors, and we shall draw further attention to them later.

Another remarkable feature presented by the table is the great discrepancy among the several families in regard to the number of species comprised in each. Thus the family Compositæ includes about 60%, Rubiaceæ about 25%, Campanulaceæ 5½%, Cucurbitaceæ 4% of the total number of species of Inferæ, while the remaining 5—6% is divided among seven small families. Evolution has ceased, if we may so express it, to make experiments on special lines to any great extent ; its trend among these higher forms is powerful and clear, namely, along that line which terminates with the group which has been most successful in the struggle for existence, the Compositæ.

Beside the relative position of the ovary, the Inferæ differ from the Bicarpellatæ in three significant features :—1st, the andrœcium is, with rare exceptions, isomerous with the corolla. 2nd, in more or less intimate connection with this, the tendency to zygomorphy in the individual flower is but rarely represented ; regular corollas are the general rule, zygomorphy, when it occurs, being usually the product of close aggregation of flowers, and appearing in the exterior

ENGLER (group)	ENGLER (family)	BENTHAM & HOOKER (group)	BENTHAM & HOOKER (family)	APPROX. NO. OF SPECIES.	ECONOMY TENDENCY — Stamens.	Carpels.	Loculi in Ovary.	Ovules per loc.	ADAPTATION TO INSECT-VISITS — Symmetry of Flower.	General Adaptations.	Special Adaptations.	SEED DISPERSAL.
RUBIALES	RUBIACEÆ	RUBIALES	RUBIACEÆ	4500	=C almost without exception	usually 2 sometimes more	usually =carpels, sometimes unilocular	1—∞	nearly always regular, rarely zygomorphic	dense inflorescences frequent; also large flowers, long corolla-tubes		winged seeds in some multi-ovulate forms; otherwise no special features
RUBIALES	CAPRIFOLIACEÆ	RUBIALES	CAPRIFOLIACEÆ	230	=C, rarely <C	sometimes 2, usually more	usually 2 or more; rarely unilocular	1—∞	tendency to irregularity in many cases	close umbels frequent		one or more calyx-lobes often large, otherwise petaloid
RUBIALES	ADOXACEÆ			1	4—1, always <C		1	1	regular			
RUBIALES	VALERIANACEÆ	RUBIALES	VALERIANEÆ	215	usually =C, sometimes <C	3, but only 1 fertile	1	1	zygomorphy and irregularity induced in the individual flower (see text)	heads	spur at base of corolla	calyx a pappus in the fruit
RUBIALES	DIPSACACEÆ	RUBIALES	DIPSACEÆ	150		2	1	1		heads		calyx & epicalyx variously modified
CAMPANULATÆ	CALYCERACEÆ	ASTERALES	CALYCEREÆ	23	=C	2	1	1	regular	heads		
CAMPANULATÆ	COMPOSITÆ	ASTERALES	COMPOSITÆ	over 11000	=C	2	1	1	zygomorphy resulting from close aggregation of flowers	aggregation into heads with zygomorphy of outer florets	*Pollen-presentation mechanism*	calyx often a pappus in the fruit
CAMPANULATÆ	CAMPANULACEÆ	CAMPANALES	CAMPANULACEÆ	1000	=C	=C to 2, inferior to half superior	usually =carpels, septa sometimes imperfect	∞	regular to zygomorphic		*Pollen-presentation mechanism*	
CAMPANULATÆ	GOODENIACEÆ	CAMPANALES	GOODENOVIEÆ	210	=C	2 inferior or partly superior	unilocular; septa sometimes imperfect	∞ to few to 1	zygomorphic		indusiate stigma ('pollen-cup')	
CAMPANULATÆ	CANDOLLEACEÆ	CAMPANALES	STYLIDIEÆ	100	2	2	unilocular; secondarily multilocular by infolded placentæ; sometimes one-celled	∞			irritable gyno-stemium	
CAMPANULATÆ	CUCURBITACEÆ	In PASSIFLORALES	CUCURBITACEÆ	650	=C or <C by fusion (see text)	3—5	unilocular; but secondarily multilocular by infolded placentæ; sometimes one-celled	1—∞	regular			

florets of dense inflorescences. This type of zygomorphy, we shall see, is not accompanied by oligomery of the andrœcium. And 3rd, the ovary is composed not infrequently of more than two carpels, although the general tendency is toward the bicarpellary gynœcium, as reflected in Compositæ. The bicarpellate pistil thus represents a tendency in progress in the Inferæ, whereas in Bicarpellatæ this tendency was already realized in their hypothetical proximate common ancestor. The completeness of this realization presented us with one of our most formidable difficulties in the way of discovering the true ancestry of the Contortæ (see chapter IV) ; and we shall find, on the other hand, that the probable ancestry of the Inferæ is not so obscure.

<p style="text-align:center">*   *   *   *</p>

RUBIALES.

This cohort consisted, in former editions of Engler's system, of the two families Rubiaceæ and Caprifoliaceæ (including *Adoxa*) only, and so coincided with Bentham and Hooker's cohort of the same name. Valerianaceæ and Dipsacaceæ were associated to form the cohort Dipsacales (Aggregatæ) ; the latter is now merged into Rubiales, with such justification as will be suggested later in the present chapter.

Rubiaceæ. Of the five families concerned, Rubiaceæ is by far the largest in point of number of species, containing nearly eight times the number included in the other families taken together. How far, however, they are to be regarded as composing a truly natural family is open to question, as will appear presently. For Rubiaceæ display a very wide range of structure, both vegetative and reproductive ; the tribe Galieæ, to which the British species are confined, is the least representative in the whole family. For the most part Rubiaceæ comprise tropical trees and shrubs, herbaceous forms, apart from Galieæ, being decidedly exceptional.

The only essential character of the rubiaceous flower which is so far constant as to rank as critical is the presence of a regular, isostemonous, epigynous,—and, of course, sympetalous—corolla ; and with this may be coupled the vegetative characters of opposite (occasionally whorled) leaves with entire margins and interpetiolar stipules (except in Galieæ). The combination of these characters in any given plant is sufficient to proclaim it a Rubiacea beyond the possibility of question.

The corolla displays in some rare cases a leaning toward zygomorphy, e.g., *Capirona, Coutarea, Ferdinandusa, Dorothea.* In

Henriquezia the corolla is bilabiate, recalling that of many Bignoni-aceæ; this includes about five species only. In other cases the corolla-tube is bent,—e.g., *Hippotis, Dichilanthe, Chasalia* ; in others, e.g., *Palicourea*, the tube is furnished with a small sac or spur at the base. In all these cases, however, the andrœcium is isomerous with the corolla, although a condition comparable with didynamy—in effect, at any rate—is observable in the insertion of the stamens at different levels (see figures of *Henriquezia*, p. 40, and *Aitchisonia*, p. 126, of Engler, *Nat. Pflanz.* IV, 4). The exceptions to the isostemonous arrangement are extremely rare, and it is open to doubt whether the relative examples are properly classed with Rubiaceæ. Such are *Carlemannia* (3 spp.) and *Silvianthus* (1 sp.), which differ further from other Rubiaceæ in having leaves with toothed margins and reduced or obsolete stipules. In the monotypic *Pravavinia* from Borneo the flowers are diœcious, and the male flowers are described as having twice as many stamens as corolla-lobes.

The character-diversity in Rubiaceæ is seen in 1st, the habit ; 2nd, the modes of attainment of conspicuousness of the flower or inflorescence ; 3rd, the number of carpels and loculi in the ovary ; and 4th, in the number of ovules contained in each loculus. This constitutes a wide field of variability as compared with any family which we have considered previously, and we are led to the *primâ facie* conclusion that Rubiaceæ may represent a relatively primitive group. In the first place the habit is as a rule arboreal or fruticose ; and we have already seen in more than one connection that this character is suggestive of relative primitiveness, among the higher Sympetalæ at any rate. Herbs, however, are not uncommon, although the herbaceous forms are confined for the most part to certain tribes, *viz.*,—Oldenlandieæ, Knoxieæ, Sperma-coceæ, and Galieæ. In the Anthospermeæ, the transition from the shrubby to the herbaceous condition is well illustrated in the series of genera ; some Spermacoceæ are suffrutescent, and Oldenlandieæ are linked with neighbouring tribes by not a few shrubby forms. Herbaceous genera of undoubted affinity, again, occur in tribes composed typically of arboreal and fruticose genera ; such are *Sipanea* and *Limnosipanea* in Rondeletieæ ; *Bouvardia* (shrubs and herbs) in Cinchoneæ ; *Coccocypselum* and *Sabicea* spp. in Mussændeæ ; *Geophila, Uragoga* (shrubby to herbaceous), and *Fergusonia* in Psychotrieæ.

A distinct tendency to the herbaceous habit is thus traceable

within the family, and roughly 22%[1] of the total number of species are herbs.

In regard to the general principle of adaptation to insect-visits, the Rubiaceæ are decidedly primitive in comparison with the groups with which we dealt in the preceding chapter. Setting aside the rare and isolated cases of zygomorphy referred to above, this adaptation is practically confined to the attainment of conspicuousness either by enlargement of the individual flower, or by aggregation into dense inflorescences. In the former case conspicuousness is frequently coupled with considerable elongation of the corolla-tube, the length of which is sometimes enormous,—*Posoqueria*, *Hillia*, *Cosmibuena*, *Randia* spp., *Gardenia* spp., etc.

Conspicuousness by virtue of aggregation is reflected primarily in the umbellate or corymbose inflorescence, which is, broadly speaking, characteristic of Rubiaceæ, especially of those members of the family which are to be regarded as most nearly representative of what we shall name the rubialian stock (*infra*); simply spicate or racemose inflorescences are quite exceptional. The aggregation displays every conceivable degree of density ; the limit is attained on the one hand in the capitula, often involucrate, of genera such as *Uragoga* (*Cephaelis*), *Schradera*, *Spermacoce* spp., etc., and especially in the globose heads of the tribe *Naucleæ* ; and on the other hand in the close axillary clusters seen, *e.g.*, in many of the tribe Spermacoceæ, which sometimes recall the verticillasters of Labiatæ. In some cases the calyces fuse together and lose their separate identity in the fruit,—*e.g.*, many *Naucleæ*, *Morinda*, etc. This aggregation, however dense, never involves in Rubiaceæ the zygomorphy of the outer florets; the latter we shall meet with in more advanced members of the rubialian plexus.

A special form of conspicuousness occurs among Rubiaceæ with sufficient frequency to be regarded as the expression of a tendency, —the foliaceous development of one or more of the calyx-lobes (*calycophylly*). This phenomenon is met with in various genera of diverse affinity, in all or some only of the species: the most familiar example is *Mussaenda*, several species of which—notably *M. frondosa* —are cultivated as ornamental plants. Inequality of the relatively large calyx-lobes is a common feature in Rubiaceæ.

In the number of carpellary leaves composing the pistil the range varies from isomery with the corolla to two, variation occurring sometimes within the limits of a single genus (*Gonzalea*, *Sabicea*,

[1] Including Galieæ, which represent about 10% (*infra*).

Hoffmania, Antirrhœa, Palicourea) ; and altogether the proportion of species with gynæcium of more than two carpels represents about 10% of the whole family. The gynæcium is thus usually bicarpellary, but the tendency to this condition is clearly traceable through a series of polycarpellary forms. In regard to the segmentation of the ovary, the unilocular condition is quite exceptional, occurring in less than 4% of the family (*Gardenia, Coussarea, Faramea, Opercularia,* etc.). In most of these cases the placentation is parietal, there being thus no evidence of the derivation of this unilocularity from the degradation of ancestral septa. There is, on the contrary, evidence of septation by the meeting of projecting parietal placentæ, e.g., *Gardenia, Posoqueria, Oxyanthus,* and others. The number of loculi, then, is usually equal to the carpel-number ; there is no indication of "secondary" septation (schizocarpy), so that there are usually two chambers in the rubiaceous ovary. In the small minority with unilocular ovary this latter condition not impossibly represents the relic in the family of a primitively unseptate ovary, and so cannot be regarded as a progressive step in the direction of the higher Inferæ (*e.g.*, Dipsacaceæ) with unilocular ovary. The suggested retention rather than the acquisition in descent of the unilocular state is parallelled in Tubifloræ, as we have seen in chapter VI.

The number of ovules in the ovary is, perhaps, the most important feature concerned in Rubiaceæ, especially in view of its employment as a criterion of the primary two-fold division of the family. Its critical value has, however, been called into question, for it involves in some cases the wide separation of forms which differ generically in no other particular save that of the number of ovules borne in each loculus of the ovary. This is illustrated in the comparison, *e.g.*, of *Webera* with *Pavetta* or *Ixora*, of *Tricalysia* with *Coffea*, of *Urophyllum* with *Lasianthus*, of the tribe Oldenlandieæ with the tribe Spermacoceæ, and so on. The tribe Naucleæ, again —apparently a very natural group—includes both multiovulate and uniovulate forms.

It must be admitted, on the other hand, that broadly speaking the members of the multiovulate series (Cinchonoideæ) differ materially in general facies from those of the uniovulate series (Coffeoideæ). Bentham and Hooker recognized a third series, characterized by the presence of two ovules in each chamber of the ovary. This section included barely fifteen species, comprised in the two tribes Cruckshanksieæ and Retiniphylleæ; but the component

genera of these tribes are quite distinct from the rest of the family. A number of the Gardenieæ section of Cinchonoideæ, however, have only two ovules in each loculus of the ovary.

On the lines adopted in these chapters, the progressive reduction in the number of megasporangia represents a definite evolutionary tendency, and, in accordance with these lines, we expect this reduction to be accompanied by evidence of other changes in the course of descent. The broad distinction between Cinchonoideæ and Coffeoideæ to which we have just alluded provides such evidence, the value of which must be measured by the amount and extent of that distinction. In the case of parallel genera like *Webera* and *Pavetta* it may be that an illustration is afforded of the working of the reduction-tendency within the limits of a single genus; and the merging of such a pair of genera into one would be quite as justifiable as the inclusion of hypogynous and epigynous forms within the single genus *Saxifraga*. The case seems to be but a particular example of a general proposition which is tacitly assumed through all our discussions of affinities, namely, that when a character represents a biological tendency at work in any particular group, it loses its critical value in the determination of affinities within that group. In Rubiales the tendency to reduction in ovule-number, and in Rosales the "Calycifloral" tendency (chapter II), represent definite biological tendencies; hence uniovulate and multiovulate forms may properly be included even in the same genus in Rubiaceæ, and hypogynous and epigynous forms in equally close connection in Rosales. A looser and somewhat misleading method of expressing the same proposition is familiar to most systematists—that the value of any character in classification depends upon its constancy; we shall have need to refer to this at the conclusion of our discussions.

We may summarize the position by the statement that the tendency to reduction in ovule-number to one per loculus is realized to a considerable degree in Rubiaceæ; over 60% of the total number of species have one ovule only in each ovary-chamber. The progress of this tendency is traceable especially in the extensive tribe Gardenieæ of Cinchonoideæ, in which the ovules tend to be relatively few in number, and the seeds correspondingly large. The occurrence of ovaries with two ovules or even one only per loculus in forms having obvious affinities with the Cinchonoideæ should not, therefore, excite surprise, although the practical value of ovule-number as a guide to the systematist is diminished

in proportion to the number of such *excepta*. This number, however, barely exceeds a score ; but the parallel genera referred to present a serious problem which calls for careful investigation. In a few very rare cases the difficulty has been successfully met—notably in the case of *Cephalanthus*, which, in spite of its uniovulate ovary-chambers, is included in the tribe Naucleæ of Cinchonoideæ ; and this doubtless because of the very characteristic globose capitula of *Cephalanthus* and all the other Naucleæ. In other cases the affinities, though they may prove clear enough on a closer investigation, are not so obvious ; and this has very probably resulted in the wide separation of species which should properly be included in the same genus.

The reduction in ovule-number, we have already stated, is not accompanied by secondary septation as in the case of the schizocarpic tendency in the Diovulatæ section of Tubifloræ (*supra*, p. 230). Nor is there any general tendency to specialization of the fruit or seed ; but in some rare instances one of the persistent calyx-lobes becomes foliaceous as the fruit develops (*Alberta, Nematostylis*, etc.) and so aids undoubtedly in its distribution. In several of the Cinchonoideæ the fruit is capsular and the seeds winged.

We have seen how varied are the Rubiaceæ in their essential characters, and the question arises whether the family as arranged at present should not properly be divided into a number of families. For the most part, however, the series of forms concerned display the several characters in so continuous a progression that satisfactory critical dividing-lines cannot be drawn ; this difficulty has just been illustrated in connection with the character of ovule-number, and the same applies to other features, such as carpel-number, inflorescence-character, etc. This state of things is in keeping with the relative primitiveness of the group, which may be regarded as the expression of extensive evolutionary activity, the reflection of tendencies at work.

In the case of at least two tribes, however, Naucleæ and Galieæ,[1] the distinction seems to be sufficiently constant and well-defined to warrant their promotion to family-rank. Either tribe can be diagnosed in practice at a glance, the first by the perfectly spherical compact capitulate inflorescences, the second by its familiar vegetative features. There are no forms among other rubiaceous tribes which might be regarded as transitional in the direction of the Naucleæ ; and their tribal characters as formulated in either of our modern systems of classification may well be accepted as the characters of a family, Naucleaceæ.

[1] Stellatæ Ray, *Synops.* 223 (1690).

We shall deal separately with Galieæ later in the present chapter.

Caprifoliaceæ. Turning now to Caprifoliaceæ, we are confronted with a family of less than 300 species consisting almost entirely of trees and shrubs, confined, in marked contrast with Rubiaceæ, to temperate climates. The two families are, without doubt, closely allied, and no critical floral characters can be prescribed to distinguish one from the other. The points of difference, we shall find, are nevertheless of great importance, but they concern tendencies and not fixed characters; they have thus little value to the practical systematist.

Caprifoliaceæ are, however, readily distinguishable from Rubiaceæ in practice by means of vegetative characters, thus:— stipules occur very rarely in the former family outside the genus *Sambucus*, and in *Sambucus* the leaves are pinnately compound; in those cases where stipules occur they are not "interpetiolar."

The critical floral characters are precisely the same as for Rubiaceæ, but there are important differences in those characters which are variable within the respective families. In the first place, Caprifoliaceæ display a marked tendency to asymmetry in the corolla, and this is reflected in half the total number of species in the family. A familiar example of this is *Lonicera*, as illustrated in the Honeysuckle, the corolla being zygomorphic in most of the species of this extensive genus; a sac, or incipient spur is frequently present at the base of the corolla. This zygomorphy is not of that type concerned with aggregation of flowers; nevertheless it is seldom accompanied by oligomery of the andrœcium (*v. supra*) in this family. Evolutionary advance has not usually proceeded to the latter length, and, indeed, the lobes are sometimes only slightly unequal in these forms with asymmetric corollas. In *Linnæa* (including *Abelia*) and *Dipelta*, however, together comprising over a dozen species, the andrœcium is oligomerous, consisting of four didynamous stamens.

The inflorescence, as in Rubiaceæ, is prevailingly umbellate or capitate, the tendency being to bring the flowers to one horizontal level, or, at any rate, to present a continuous surface to insect-visitors, which consequently may readily pollinate several flowers in a single visit. It will be convenient hereafter to refer to inflorescences which display this tendency as "umbellifloral" inflorescences. This tendency is no more than the concomitant of that general tendency to aggregation which is the mark of Umbelli-

floræ; and the importance of this consideration will become manifest when we premise that it is to an umbellifloral ancestry that we shall find reason to refer the rubialian stock (*infra*). Caprifoliaceæ are especially interesting in this regard, as they exhibit the tendency to form a rayed inflorescence comparable with that in Umbelliferæ and Compositæ. Thus in our British *Viburnum Opulus* the outer flowers of the dense flat-topped cymes are large, oblique, and sterile, the whole inflorescence tending to become the biological equivalent of a single flower.

The ovary in Caprifoliaceæ, in contrast with Rubiaceæ, consists of more than two carpels in as many as 75% of the total number of species; the most usual number is three,—a common number for polycarpellary ovaries generally (see chapter II). The number of loculi is usually equal to that of the carpels; but a feature of special interest is the frequently-occurring phenomenon of degradation of all save one of the loculi when the ovary comes to maturity. This is well illustrated in *Viburnum*, and a transitional state occurs in the tribe Linnæeæ; in *Linnæa* there are two effete ovules in each of two of the three ovary-chambers, and one only in the third, the latter alone maturing as a seed. A condition similar in kind is found in *Symphoricarpus* and *Dipelta*, the other two genera of the tribe; and this tribe, comprising twenty species or more, may be regarded as representing the mean between those forms with many ovules in each ovary cell (*Lonicera*, *Diervilla*, etc.), and those with only one (*Viburnum*, *Sambucus*, etc.) In *Lonicera* the number of ovules is usually few, sometimes two only; so that, as in Rubiaceæ, there is a continuous series of forms illustrating the progression from the multiovulate to the uniovulate condition. About half the species in the family are characterized by the latter, and the Linnæeæ represent together less than 10%.

The fruit displays no marked specialization; it is usually a berry or drupe, rarely a capsule (*Diervilla*).

* * * *

The two families which we have just considered are clearly linked in close affinity, and in view of the wide range of their essential characters, coupled with their prevailingly woody habit, we have been led to conclude that they represent a relatively primitive stock, the Rubialian Stock. Into the origin of that stock we must presently enquire; but it will be convenient first to examine its immediate progeny, the herbaceous.

DIPSACALES.

In Caprifoliaceæ are foreshadowed unmistakeably those features which characterize this progeny, namely, irregularity of the individual flower and reduction of the ovary-cells to one containing a single ovule.   In so far as these characters have become fixed in Valerianaceæ and Dipsacaceæ they may be regarded not unreasonably as the criteria of a separate cohort, as in earlier editions of Engler's Syllabus, representing a branch-stock, which we may name conveniently the Dipsacalian Stock (see diagram, p. 230). They seem, nevertheless, to be as fairly entitled to a place in the same cohort with Caprifoliaceæ as, say, Labiatæ with Bignoniaceæ, or Asclepiadaceæ with Loganiaceæ.   In any case their place among the descendants of the rubialian stock seems to be unchallengeable, and their herbaceous habit is in keeping with their relative advance.

In Valerianaceæ the tricarpellary ovary with but a single fertile loculus already noted among Caprifoliaceæ is the invariable rule ; and the other tendency of the tribe Linnæeæ (*supra*)—oligomery of the andrœcium—is realized and becomes a fixed character. The number of stamens may be one, two, three or four, according to the genus, but it always falls short of the number of corolla-lobes.   The irregularity of the corolla foreshadowed in Caprifoliaceæ is carried through every degree of transition in Valerianaceæ, from the sub-regular type seen in species of *Valeriana* with small sac or spur or none, to the long-spurred type seen in *Centranthus*, where the floral asymmetry is enhanced by the reduction of the andrœcium to a single stamen.   This type of asymmetry must be regarded as induced in the individual flowers by insect-visits, and not as the result of aggregation.   The inflorescence is usually more or less lax, of the " umbellifloral " type, but the extreme development of this type—capitate or sub-capitate—is not uncommon.

It is in Dipsacaceæ that the climax of the aggregation-tendency is seen, for in this family the inflorescence is almost invariably an involucrate capitulum similar to that of Compositæ.   Further, zygomorphy of the outer florets results in many species in the formation of a " ray " series ; this zygomorphy is, of course, of that type which is the outcome of aggregation.   The other type of zygomorphy, foreshadowed in Caprifoliaceæ and elaborated in Valerianaceæ, characterizes Dipsacaceæ also, so that in the last-named family both our types of zygomorphy (chapter I) are present in the same plant, the same inflorescence, and conceivably even in the same individual flower.

A further climax is reached in regard to the ovary; in the flower of Dipsacaceæ the two sterile carpels of Valerianaceæ have entirely disappeared, the net result being a unilocular ovary containing a single pendulous ovule; but according to Payer[1] a second carpel makes its appearance in the ontogeny of the flower, so that the ovary is developmentally bicarpellary.

The andrœcium in Dipsacaceæ consists usually of four stamens, diandrous species being of rare occurrence (*Scabiosa* spp., *Morina* spp.), and is probably in all cases oligomerous.[2] Progressive reduction of the andrœcium is observable within the genus *Morina*.

The calyx in both Valerianaceæ and Dipsacaceæ displays considerable specialization in relation to fruit-dispersal. In the latter family it consists of two whorls (three in *Triplostegia*) which persist in the fruit as prongs, wings, and so on, thus aiding in its locomotion. In Valerianaceæ the calyx is obsolete in the flower (except in *Nardostachys*), but reveals itself in the fruit in the form of bristles, or a feathery crown. This calyx-specialization is intimately associated with the dense aggregation of flowers, as is especially apparent in the case of Compositæ. In a close inflores- cence the mere crowding of the florets provides a source of mutual protection among them ; and the calyx, being no longer required for purposes of protection, is pressed into the service of fruit-dispersal.

Dipsacaceæ and Valerianaceæ represent ultimate branches in the evolutionary tree of Inferæ, and we must retire to lower branches for the purpose of tracing their connection with the other groups (see diagram, p. 230). In our backward course we are confronted with the problem of the archichlamydeous stock from which Inferæ have been derived ; and first let us enquire into the origin of that group with which we have already dealt, the Rubiales.

<p align="center">*　　*　　*　　*</p>

ORIGIN AND AFFINITIES OF RUBIALES.

We have hinted already that Umbelliflorae is the group which is the most closely allied to the archichlamydeous ancestors of Rubiales ; and a comparison between these two cohorts goes far to substantiate this suggestion.

The essence of both groups is epigyny on the one hand and the " umbellifloral " inflorescence on the other ; both these charac ters

[1] Payer: *L'organogenie comparée de la Fleur*, p. 630.
[2] Eichler (*Blüthendiagramme*, I, p. 280) maintains that tetramerou corollas in Dipsacaceæ are the product of fusion of tw members of a primarily pentamerous whorl.

reflect broad tendencies of biological progress. The advanced position of Umbellifloræ relatively to Archichlamydeæ has been pointed out in chapter II; they stand in the foremost rank of advance along all the general evolutionary lines of that series, namely, the "calycifloral" line, the line of aggregation with zygomorphy of external flowers, and the line of economy in reproductive parts. Within both cohorts the progress from a polycarpellary to

COMPOSITAE

DIPSACACEAE

VALERIANACEAE

UMBELLIFERAE

CANTOLLEACEAE　　BRUNONIACEAE

ADOXACEAE

GOODENIACEAE　　　DIPSACALIAN
STOCK

CAPRIFOLIACEAE

CAMPANULACEAE

CALYCERACEAE　　　RUBIACEAE

ARALIACEAE

CORNACEAE

CUCURBITACEAE

RUBIALIAN
STOCK

UMBELLIFLORAL
STOCK

CAMPANAL
STOCK

—C A L Y C I F L O R A L—

—P L E X U S—
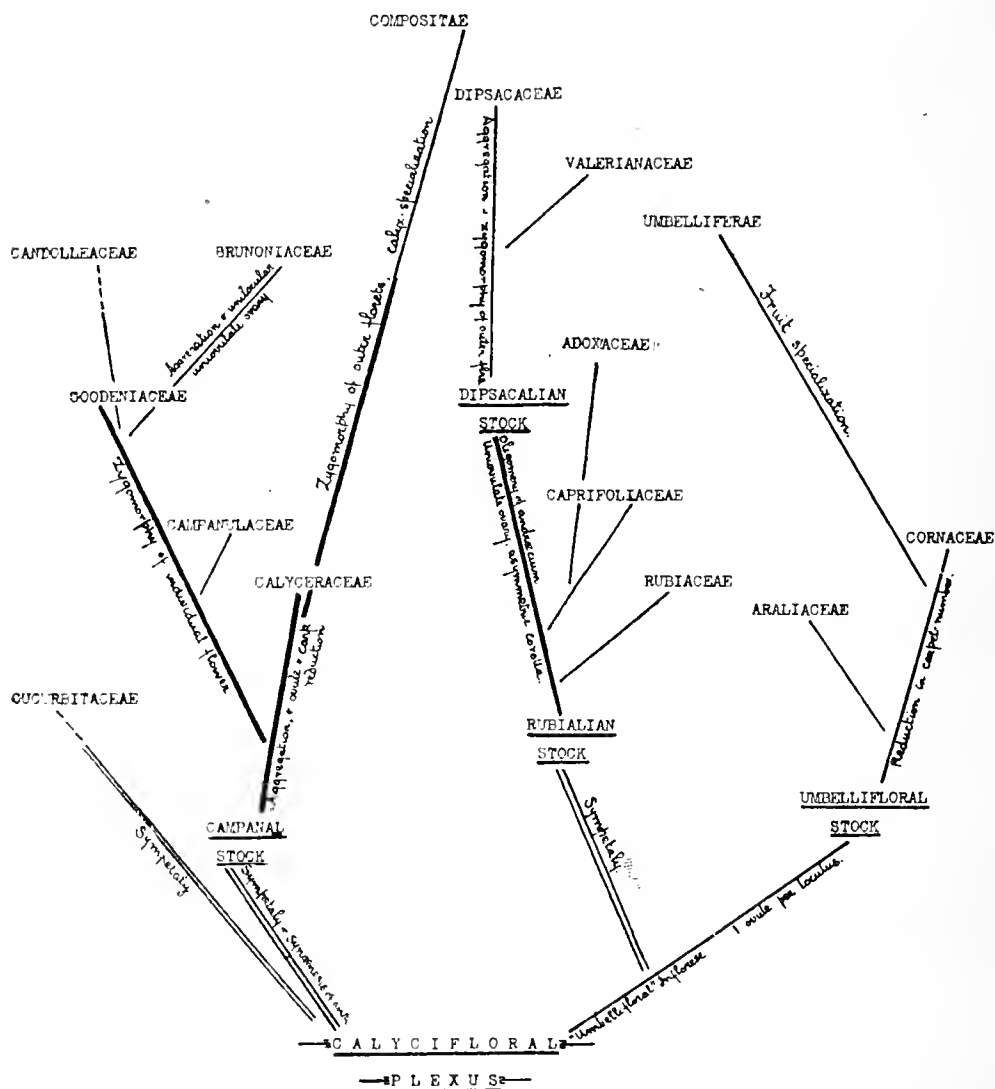
a bicarpellary gynæcium is observable; in both the ovary is only very rarely unilocular; and in both the androecium is primitively isomerous with the corolla, and the latter primitively regular. In the last-named connections the rubialian tendency of irregularity in the corolla coupled with oligomery of the androecium has given rise to Valerianaceæ and Dipsacaceæ; this tendency distinguishes Rubiales from Umbellifloræ, where it is non-existent.

But the prime distinction between Rubiales and Umbellifloræ rests upon the constant sympetaly of the former, and the constant presence of a single ovule only in each loculus of the ovary in the latter. Umbellifloræ may be regarded as the representatives of a side-branch from the calycifloral (rosalian) plexus, determined by the complete realization of the calycifloral tendency of the latter, and by the umbellifloral type of inflorescence together with the reduction of the ovules to one per ovary-cell. Before the latter tendency was fully realized, a side-branch determined by sympetaly emerged, terminating with the Rubialian Stock.

The suggested trend of evolution is indicated in the accompanying diagram. The existing groups nearest to the Umbellifloral stock are the woody Araliaceæ and Cornaceæ,—especially, perhaps, the former, in which the number of carpels exceeds two in the flowers of 75% of the family (*i.e.*, over 280 species). From the end of the line of progressive reduction of the carpels to two the side-line to Umbelliferæ emerges, dominated by further elaboration of the inflorescence, the formation of "ray" florets, and fruit-specialization. The Umbelliferæ, moreover, are mostly herbaceous, a condition already alluded to as usual among the most advanced members of the progeny of particular stocks among the higher flowering plants ; analogies to the relationship between Umbelliferæ and the woody Araliaceæ are afforded by Labiatæ and Verbenaceæ, by Asclepia-daceæ and Apocynaceæ, by Dipsacales and Rubiaceæ, and so on. In fact, the growing shoots in the evolutionary tree, just as in a natural tree, are woody at the base and herbaceous at the tip.

The single offshoot from the Rubialian Stock is determined by the tendency to irregularity in the corolla, oligomery of the andrœ-cium, and a uniovulate ovary, and leads to the Dipsacalian Stock. Low down upon this offshoot a short branch arises leading to Rubiaceæ, the living representatives of the Rubialian Stock; further up, already exhibiting traces of the dipsacalian tendencies, appears the caprifoliaceous branch. Starting from the Dipsacalian Stock, aggregation with zygomorphy of outer florets leads to Dipsacaceæ ; while Valerianaceæ, with excessive asymmetry but with traces of an ancestral polycarpellary ovary, represent the closest existing approximation to the Dipsacalian Stock.

✳   ✳   ✳   ✳

The Rubiales present one or two interesting and familiar problems which are scarcely within our province, but which we may

not leave altogether without notice; such are the affinities of the
tribe Galieæ of Rubiaceæ, of *Sambucus*, and of *Adoxa*.

Galieæ.   Special attention has naturally been devoted to
Galieæ as the sole representatives of Rubiaceæ in our own latitudes;
and it is to be feared that much of the significance underlying the
typical features of this extensive family has been overlooked in the
stress which has been laid on this very untypical tribe.   The Galieæ
represent approximately one-tenth of the Rubiaceæ as arranged in
our modern systems of classification; and their floral characters,
which are remarkably constant, entitle them without doubt to a
place in that family.   Their weakly herbaceous habit, insignificant
flowers with reduced calyx and regulary bicarpellary ovary, the
frequent reduction in the number of flowers in the primary umbelli-
floral inflorescence, and the specialized fruit, point to the con-
clusion that the Galieæ form a specialized and rather retrograde
section of Rubiaceæ.   In vegetative characters, however, they are
distinct from the rest of the family, and the practical test of
interpetiolar stipules breaks down; for the shoot consists of whorls
of foliar organs arranged at intervals along the weak stems, and
there is no trace of structures which can be designated stipules
without hesitation.   The gulf between this condition and that
which is typical of Rubiaceæ has been bridged in modern systems
by the supposition, not altogether unwarranted, that some of the
foliar organs in a whorl represent stipules.   This supposition,
however, is still far from complete justification; an excellent
discussion upon the matter is contained in Lindley's *Vegetable
Kingdom* (3rd edition, pp. 768-771).   In any case the question
concerns for the most part the vegetative organs; and whatever
be the true homology of the foliar appendages, the general
facies of the Galieæ seems to entitle them to separate family
rank,—at any rate if vegetative features alone may rank as critical
family characters.   Their reduced calyx (*Sherardia* excepted),
divergent styles, and didymous fruit would go to support this rank;
and the distinction between " Galiaceæ " and " Rubiaceæ " [1] would at
least be as satisfactory as that between Rubiaceæ and Caprifoliaceæ.

[1] If Galieæ be separated from the rest of the Rubiaceæ, the name
Rubiaceæ would have to go with it, as it includes the genus
Rubia.   The nomenclature would need to be some such as
Lindley's—Galiaceæ and Cinchonaceæ—or better, as retaining
the long-established name, Rubiaceæ and Cinchonaceæ.   This
would at least have the merit of making the European
" Rubiaceæ " representative of the family!

Affinities of Caprifoliaceæ : Sambucus. As we have remarked already, the distinction between the flowers of Caprifoliaceæ and Rubiaceæ is not critical. Here again we are driven to vegetative characters as criteria; and in general facies the constantly her-baceous Galieæ differ much more widely from the rest of the Rubiaceæ than do the woody Caprifoliaceæ. Moreover the flowers in the latter family display a range of diversity in essential characters even greater than that exhibited among Rubiaceæ.

In this connection, as with Galieæ, a great deal of stress has been laid on a single vegetative character—stipules. The presence or absence of these organs is the sole constant feature of distinction between Rubiaceæ and Caprifoliaceæ, and even this fails in the case of *Sambucus*; but the latter differs from Rubiaceæ, from the rest of Caprifoliaceæ, and indeed from most sympetalous shrubs and trees, in having compound leaves. In virtue, apparently, of its stipules alone, *Sambucus* has been regarded by some botanists as a link between Rubiaceæ and Caprifoliaceæ. The need would seem to be to discover a gulf rather than a link between these two families, at least from the aspect of progressive evolution. *Sambucus* has further been considered as relatively primitive, and as affording the way through which the connection between the epigynous Sympetalæ and the epigynous Polypetalæ may be traced. The 3-5-locular ovary with a single pendulous ovule in each loculus, and the branching of the leaf-lamina are characters which suggest affinity with Araliaceæ, apart from the general umbellifloral characters which *Sambucus* shares with other Caprifoliaceæ; and it may be that this genus is of all the Rubiales one of the most nearly allied to the umbellifloral stock. But the question is scarcely of primary importance for our purposes, and we may dismiss it with the suggestion that if *Sambucus* it to be separated from Caprifoliaceæ as a distinct family, then Galieæ should certainly receive similar treatment.

The value of stipules in classification. The foregoing has suggested a question of somewhat serious importance in regard to the Rubiales, namely, the phyletic value of stipules. On the face of it, it is difficult to conceive that a minor vegetative character can have any material weight in broad general considerations of phylogeny. Indeed, the character must needs be disregarded in the recognition of the descent of Rubiales from an umbellifloral ancestry, for in Umbellifloræ stipules are conspicuous by their absence; similarly the arrangement of the leaves upon the axis must be set

aside in the same connection, for the leaves of Umbelliflorae are
mostly alternate.   Yet stipules of that characteristic interpetiolar
type, and leaves opposite (occasionally whorled), simple, and with
entire margins occur without exception in 3,500 species which are
linked in a more or less close circle of affinity,—*i.e.*, Rubiaceæ
excluding Galieæ.   This constancy of vegetative characters in so
large a group is without parallel in the whole series of flowering
plants, and seems to call for some biological explanation; but the
writer is unaware that any has been proffered.   It may be that
the stipules, which are often connate into a sheath, exercise an
important function in bud-protection, in relation to the damp
tropical conditions under which Rubiaceæ nearly always grow ; in
this case fusion of the stipules might well constitute a " tendency "
to the formation of a much-needed sheath or cap.   This contention
receives some measure of support in virtue of the fact that the
stipules are rapidly deciduous in many cases; while in Galieæ, the
sole extensive rubiaceous group which inhabits temperate climates,
interpetiolar stipules do not occur.   It is conceivable that the
stipules of the tropical Rubiaceæ, being no longer required for the
peculiar function which they discharge in a hot damp climate,
became foliaceous and assumed an assimilatory rôle in the course
of evolution of these Rubiaceæ of temperate habitats.   The variable,
sometimes large (8 or 9) number of foliar organs in a whorl in
Galium and its allies, is explicable on the ground of partition of
originally simple interpetiolar stipules; bipartite and multipartite
stipules are far from uncommon among the tropical Rubiaceæ.

Interpetiolar stipules occur elsewhere among Sympetalæ only
in Loganiaceæ,[1] and, indeed, the latter family have been described
as Rubiaceæ with a superior ovary ; but it must be remembered
that both families represent relatively primitive groups and display
considerable diversity in their characters, so that a certain similarity
between them is not surprising.   Epigyny is in this case an important
critical character, and, on the lines we have followed throughout
our investigations, we are led to regard Loganiaceæ (chapter IV)
and Rubiaceæ as belonging to widely different circles of affinity.

We can venture no further than the suggestion that this
peculiar type of stipule determines merely those special lines of
descent which have led to the two families in question from their
respective immediate stocks.

[1] So-called " interpetiolar lines " unite the two leaf-bases across
the stem in some Apocynaceæ (*Tabernæmontana*).

Adoxa. We must dismiss the monotypic *Adoxa* with little more than a passing reference. Like many other forms whose characters suggest reduction in descent (*Adoxa* is essentially geophilous in habit), the affinities of this curious genus are obscure, and this largely owing to the doubtful nature of the perianth. If the outer whorl of the latter be a true calyx, then *Adoxa* should properly be classed with epigynous Sympetalæ; and its multilocular multistylar ovary with one pendulous ovule in each loculus maturing to a berry-like fruit, coupled with its capitate inflorescence of regular flowers, point to the probability of its umbellifloral ancestry and consequent affinity with the descendants of the Rubialian Stock. Its place is so indicated in the diagram, p. 230; and its extreme specialization is seen in the definiteness of the number of flowers in the inflorescence, which is most usually five, in the regularly pentamerous arrangement of the lateral flowers and tetramerous terminal flower, and in the constantly bipartite stamens.

<p align="center">*   *   *   *</p>

This completes our review of the Rubiales. We have seen that their origin is readily referable to a well-defined archichlamy-deous ancestry represented by Umbelliflorae. The latter has been regarded as an offshoot from the calycifloral plexus typified in the heterogeneous Rosales. The other cohort of Inferae, Campanulatæ, will form the subject of the next chapter.

<p align="center">[*To be continued*].</p>

THE INTERNATIONAL PHYTOGEOGRAPHICAL EXCURSION IN THE BRITISH ISLES.

IX.—THE FLORA OF GREAT BRITAIN COMPARED WITH THAT OF CENTRAL EUROPE.

BY OSCAR DRUDE

(Dresden).

AFTER a long botanical journey through a region which, in spite of its strong floristic affinity with Central Europe, is nevertheless full of a peculiar character of its own, the comparative phytogeographer is glad of the opportunity of defining his most important impressions. And this, not only because they are new to him personally, but because, however much he may have studied the literature beforehand, the impressions so obtained can never possess the same sharpness as those gained directly from nature. Perhaps, also, it will not be without interest to English floristic botanists and ecologists to learn what a German botanist has seen in their country so richly adorned with a flora of the most varied charm, and what has appeared to him different from the arrangement of the closely allied plant-formations which occur in Germany. And apart from any value which such a summary—necessarily condensed and aphoristic—may possess in itself, I undertake it the more gladly in the hope that I may in this way repay a small part of the common debt of gratitude which we foreign botanists owe to our English guides, by whom we were so kindly invited and so ably led. Space does not permit me to deal more fully with this debt of gratitude as I personally feel it, but it is a special pleasure that these brief remarks should appear in Tansley's journal, and that they should be based on his *Types of British Vegetation* and on Claridge Druce's *List of British Plants*, since these two works provided the literary basis for the observations and notes made in the course of the five weeks' tour. Just as Tansley and other members of the British Vegetation Committee, to all of whom I should like here to express my thanks, led the whole expedition over hills and valleys, through swamps and moors, from coast to coast, finishing with the ancient beeches and yews of southern Hampshire, so Druce was, as it were, a living herbarium of the flora of Great Britain, untiringly furnishing us at all times with the (not always simple) definitions of species.

SPECIES LIMITS AND LOCAL RACES.

This last task is both difficult and important. It constantly leads us into fresh paths, and in more recent times appears to have become more confused rather than clearer, since the views held in different countries and by different authors as to the extent of the limits of single species differ from one another more widely than was formerly the case. The confusion has been greatly added to by preposterous changes in nomenclature, which pursue their course in the vain hope of attaining a goal that will satisfy everyone. At the same time the complexity of the subject has naturally been increased by new phylogenetic and ecological studies. Thus it is evident that a book like H. C. Watson's *Topographical Botany*, at one time authoritative, is no longer a safe guide, even in fundamentals, and that Druce's "List" with its additions of sub-species and varieties is indispensable. In the variability of species we are confronted by old questions in a new form, especially such questions as whether variations of the same character over wide areas really belong together, or whether they are not rather made up of similar ecological variants of independent local origin, analogues to one another in various separated parts of the whole area, and thus have not the status of a single monophyletic race or sub-species.

Let me cite a single instance. The question arose as to whether a form of *Salsola Kali* occurring on the Southport dunes was to be considered as *S. Tragus.* Druce's list does not consider this form as indigenous. It is interesting to recall the doubt which such critical observers as Mertens and Koch[1] felt a hundred years ago on this "species" established by Marschall von Bieberstein, and how they tried to express its characters in a diagnosis. But it appears much more probable that the Tauric-Siberian and West European forms are local and analogous, not forming directly connected series, and that the circle of variation of each is thus to be drawn more narrowly. For this reason it was very valuable to hear an expression of the views of the English specialists on the limitation of the range of variation of their species. Very many common species constantly polymorphic in their German stations appeared to me to look very different in England, to represent in fact slightly differentiated examples of local endemism. How otherwise can we interpret the Birches for instance? How difficult it appears to be satisfactorily (it is not permissible to say "correctly") to limit the range of variation of *Betula odorata, pubescens* and

[1] Deutschlands Flora, 2, pp. 321-2.

verrucosa! How much we learned even on the first day at Cambridge
from Dr. Moss in his interesting demonstrations of the South
English forms of *Ulmus*.

To bring these fragmentary remarks to a conclusion, I may say
that I gained the impression of numerous slightly differentiated
local forms, endemic in England, and I think the study of such local
forms can scarcely be satisfactorily developed in the herbarium, but
belongs rather to the local floras of geographically and ecologically
separate regions. *Œnanthe fluviatilis* Colem. which we saw so well
in the River Cam, is given in Druce's List as an " endemic " species
for thirty-one British and two Irish counties. If the same form
occurs also in south-west Germany, the fact indicates that analogous
ecological conditions have led to analogous " races " rather than
that the same race has such a discontinuous distribution ; and one
may expect the identity of the forms to be incomplete.

UNIFORM FLORISTIC DISTRIBUTION IN THE BRITISH ISLES.

The question arises if the conditions of vegetation over the
larger portion of the British Isles are so uniform as to furnish the
conditions for the development of characteristic forms in this not
inconsiderable area from the general stock of the west and north
European flora which has been present in or has invaded the country
since the Ice Age. I am inclined to answer this question in the
affirmative in spite of the fact that Great Britain falls into a series
of well-marked floristic regions.[1] At least on the lower hills, up to
a height of about 100 m., there is apparent a uniformity, markedly
differing from what we find in Mid-Germany, in the English and
Scottish, and to some extent also in the Irish flora. Thus we find
the same species distributed throughout the whole country to a much
greater extent than we should expect over a range of nine degrees
of latitude. And the cultivated areas, from the south of England
to the valleys of the Grampians, contain species, whose growth is

[1] Thus there are the warm south-east of England with beechwoods
on the slopes of the "Downs"; the east, drained by the
rivers Ouse, Cam and Nene, with only 55 cm. of annual rain-
fall and a more continental climate ; the Atlantic south-west
(Cornwall) ; the similarly situated part of Ireland, which has,
however, higher mountains; the limestone region of the north
of England, in which *Sesleria cærulea* occurs in spite of its
curious absence from the south ; and the fine mountain regions,
differing from one another in many respects, with summits up
to and exceeding 1000 m., from Glamorgan northwards through
Wales (which we unfortunately could not visit), the Pennines,
the mountains of Westmoreland and Cumberland, and finally
the crown of all, the Grampians, which formed the northern
limit of our tour.

clearly favoured by the climate, partly of mid-German origin and partly consisting of aliens which in Germany flourish scarcely any-where in the open. Of the latter I will only mention *Araucaria imbricata*, whose fresh and flourishing appearance in the whole region of the Tay and in the gardens on Loch Tay itself, struck me very much, and *Acer Pseudoplatanus* whose magnificent growth is less remarkable, with *A. platanoides, Larix* and north-west American Conifers. The Sycamore is not wild in Great Britain, but spreads freely from self-sown seed, and, in the region of the Tay and even further north, attains dimensions which excite wonder and envy in one who is so familiar with the tree in his own mountains between Hercynia and the limit of deciduous forest in the Alps. Since *Acer campestre* is the only native species of the genus occurring in the British Isles, it is clear from this example that the country furnishes instances of *vegetational limits determined by developmental but not by climatic or ecological conditions.* Migrations are not com-pleted, capacity for dispersal is not exhausted. It is difficult to say what circumstances have been effective in influencing the migrations of great trees with wind-borne seeds, such as *Acer Pseudoplatanus, A. platanoides, Picea excelsa, Abies alba.* It is seen here very clearly, that the often cited powers of distribution of seeds appear to be much greater theoretically than they prove to be in practice. By species which, when we consider the conditions obtaining in mid-Europe, I consider unexpectedly widely distributed through Great Britain, I mean such forms as *Ulex europæus, Genista anglica, Erica Tetralix* and *cinerea, Myrrhis, Hippocrepis, Aquilegia. Ulex Gallii* goes at least as far north as Roxburgh; *Sagina nodosa* occurs from Cornwall to the Shetland Islands, though "its localities are rather dotted over the island than really continuous like those of the daisy *(Bellis)* and other more truly common species" (Watson, Topogr. Bot., p. 73). Even *Tamus communis*, which in Germany only touches the south-west, though it climbs in the alluvial woods of Strasburg with great luxuriance, is spread throughout England up to the Scottish border. *Wahlenbergia hederacea* occurs fairly continuously from Cornwall to the Scottish lowlands (56°N.) and beyond to Argyll. Nevertheless the northern mountains at about 55°N. do *in many cases* set a limit to the southern species, as in the case of *Tamus*, of which Watson says (Topogr. Bot., p. 407) "apparently quite absent from Scotland, although so nearly general to the counties of England."

These considerations may be emphasised by the following lists

taken from certain important genera, which may serve to bring into prominence a topic that has not hitherto received sufficient attention.

SPECIES REMARKABLE FOR THEIR OCCURRENCE IN THE BRITISH ISLES AND IN WEST-CENTRAL EUROPE.	SPECIES REMARKABLE FOR THEIR ABSENCE IN THE BRITISH ISLES.
Thalictrum minus, Brit. 32, Hib. 20[1]	*T. aquilegifolium* (in Germany occupies an area similar to that of *Cirsium hetcrophyllum*).
Pulsatilla vulgaris(=*A n c m o n e Pulsatilla*), Brit. 19.	
Anemone nemorosa (common to Northern Scotland & throughout Ireland).	*A. ranunculoides.*
Helleborus viridis var. *occidentalis* Brit 27.	*Ranunculus lanuginosus.*
H. fœtidus, Brit. 23.	*R. nemorosus.*
Trollius europæus, Brit. 63, Hib. 3.	*Nigella.*
Aquilegia vulgaris. Brit 64, Hib. 31.	
Aconitum Napellus, Brit. 5.	*A. Lycoctonum, Cammarum.*
Actæa spicata (York and Westmoreland).	
Corydalis claviculata, Brit. 87, Hib. 5 (Denmark to Spain).	*C. cava, C. solida, C. fabacea.*
Genista anglica, G. pilosa, G. tinctoria.	*G. germanica.*
Trifolium medium, T. ochroleucum.	*T. montanum, T. alpestre, T. rubens, T. hybridum.*
Astragalus glycyphyllus, Brit. 69.	*A. cicer, Onobrychis.*
A. danicus, Brit. 45.	
Hippocrepis comosa, Brit. 47 !	*Coronilla varia, C. montana, C. vaginata.*
Onobrychis viciæfolia, Brit. 33.	
Vicia Orobus, Brit. 37 from Devon to 57°N.	*V. cassubica.*
V. sylvatica, Brit. 82, Hib. 22.	*V. dumetorum.*
V. lathyroides, Brit. 56, Hib. 6.	*V. tenuifolia.*
Lathyrus montanus, Brit. 108!	*L. vernus. !*
L. silvestris, L. niger, L. hirsutus, L. palustris.	*L. platyphyllus, L. hcterophyllus,* etc.

[1] Number of Watson's counties in England, Wales and Scotl (Brit.), Ireland (Hib.)

Species Remarkable for Their Occurrence in the British Isles and in West-Central Europe.	Species Remarkable for Their Absence in the British Isles.
Sanicula europæa.	*Astrantia,* naturalised only.
Eryngium campestre.	
Bupleurum falcatum, etc.	*B. longifolium.*
Myrrhis odorata, Brit 66, Hib. 13 !	
	Selinum carvifolium (only Brit. 2-
Meum athamanticum, Brit. 30.	*C. aromaticum, C. aureum* (indigenous in Scotland ?), *C. hirsutum.*
Chærophyllum temulum.	
Libanotis (=*Seseli Libanotis*), Sussex, Herts., Cambs.	*Seseli* spp.
Peucedanum palustre, officinale (rare).	*P. Cervaria, Oreoselinum.*
Leucojum æstivum (rare).	*Laserpitium Siler.*
	L. vernum, naturalised only.
Paris quadrifolia (Somerset and Kent to Scotland).	*Maianthemum bifolium* (perhaps wild only in Yorks.)
Fritillaria Meleagris, Brit. 22.	*Lilium bulbiferum, L. Martagon.*
Gagea lutea.	*Gagea* (all other species).
Scilla verna, S. autumnalis.	*Anthericum Liliago.*
Colchicum autumnale.	*A. ramosum.*

German Species with Striking British Distribution.

Species.	Germany.	Great Britain.
Phyteuma spicatum ...	Common up to the N.W.	One or two localities in the S.E.
P. orbiculare ...	Montane: finishes towards the N.W. (Harz)	South English: chalk downs.
Campanula latifolia...	Montane, not in N.W.	Surrey & Gloucester to Central Scotland; on the whole sub-montane.
C. Rapunculus ...	Widely spread ...	Doubtfully wild.
Primula elatior ...	The commonest species on siliceous soils	Only in four counties round Cambridge: on chalky boulder clay and in alluvial fens.

SPECIES.	GERMANY.	GREAT BRITAIN.
P. officinalis... ...	On calcareous soils, quite absent from N.W.	Through the whole of England to Scotland: no marked soil preference.
P. vulgaris (acaulis)	Absent between the Alps and the north coast, though common in France ...	The commonest species throughout the British Isles.
Cirsium oleraceum ...	Common in alluvial meadows up to East Friesland ...	Absent.
C. anglicum (britannicum)=C.pratense	Rare in East Friesland : otherwise absent	Occurs in 49 English and 40 Irish counties : local.
C. heterophyllum ...	On siliceous soils. Montane up to Thuringia, Baltic region.	On siliceous and calcareous soils from Glamorgan to northern Scotland.

This list might be very greatly extended, but it suffices to indicate the material available for the developmental study of the flora.

Although for the sake of contrast a few West European species, such as *Corydalis claviculata*, have been introduced into these lists, yet it may safely be stated that the great bulk of the species common to Great Britain and Central Germany consists of *species with a wide montane distribution in Central Europe*, often extending towards the east or into the Alpine countries. The lists may help to give an idea how apparently capriciously Great Britain has made her selection of these species. The question is worth some discussion, because certain important factors in distribution, which have not yet received attention, are involved.

ORIGIN OF THE BRITISH FLORA.

At the meeting of the British Association at Portsmouth (where we were handsomely entertained as guests of the Mayor at the conclusion of our journey) we had the pleasure of joining in the stimulating discussions of the Botanical Section. Clement Reid, in a paper read before this Section, developed with much acuteness an argument in which he answered the question of the origin of the British and Irish flora by supposing that the arctic-glacial element of the flora present after melting of the ice was enriched from the

neighbouring continent by immigration due to dispersal of continental species by wind, birds, etc. Without wishing to deny the existence of this factor, I consider *the mixture of floristic elements already present in England at the close of the Baltic ice period*, which forms, for Germany, the starting point of the last great transformation of vegetation, *as very important.* In the southern part of England, which remained free of ice at the time of the greatest extension of glaciers, and which in the last (Baltic) ice period would have possessed mild climatic conditions on account of its maritime situation, *I consider the ground stock of species to have been settled.* The species of this stock afterwards extended further north, and constantly won fresh ground from the northern floristic elements. According to this view the flora of Great Britain would still to-day give an indication as to the distribution of species at that time, a distribution which was much more freely and profoundly modified on the continent owing to the stronger influence of the Steppe period. Thus many species, such as *Digitalis purpurea, Meum athamanticum, Thlaspi alpestre, Helleborus foetidus,* range from the Pyrenees and Western Alps through France and Belgium, on the one side to Scotland, on the other eastwards to the Harz, Thuringia or Saxony, but stop at the Sudetes, which stood completely in the line of the Ural-East Baltic invasion characterised by *Ledum, Vaccinium uliginosum, Carex pauciflora, Betula nana* and *Pedicularis sudetica.* In addition there are many other species of common mid-European distribution, and the occurrence of these in the British Isles with an increasing distribution towards the north and west gives very important indications which have hitherto not been sufficiently considered. It is also noteworthy that most of the plants given in the list above are absent from Cornwall and appear first in Devon, Somerset and Dorset (for instance so common a plant, distinguished by its preference for cool damp soils, as *Geum rivale*). Others are such common German hill plants of drier ground as *Potentilla verna*, which begins in the English "continental" region round Cambridge and preferring the east of England reaches as far north as Edinburgh. All this makes very much more the impression of an ordered distribution than of chance invasion; but the latter factor has also no doubt been always at work. The views expressed by Clement Reid are based mostly on single very remarkable species (such as *Arbutus, Daboecia, Erica vagans* and *ciliaris,* which are very isolated) and neglect the distributional relations of the great bulk of species, which we must consider in

attempting to explain the striking absence of characteristic species of the various plant-associations.

ARCTIC-ALPINE ELEMENT.

The distribution of the arctic-alpine element through Great Britain is also of very great interest, both on account of the low altitude of the stations of many species and of their concentration in definite parts of the country. The very useful tables published by E. Warming[1] on the Flora of Greenland, Iceland and the Faroës in comparison with North America, North and Mid-Europe and Siberia, furnish a basis for my calculations. Of the very great number of northern species occurring in the British Isles, forty-four are confined, within the British Isles, to the higher mountains: of these, nine are absent from the mid-European mountains (Sudetes, Hercynia, etc.) and from the Alps, and are in this sense arctic, e.g., *Poa arctica* (*flexuosa*) and *Alopecurus alpinus*. But of the much greater group of British species which are scattered through the hills and moors of the islands, (such as *Dryas*, *Primula farinosa*, *Selaginella spinulosa*, *Pinguicula*, etc., etc.) fourteen are likewise absent from the "arctic" areas of mid-Germany and from the German Alps, e.g., *Aira alpina*, *Carex pulla* (*saxatilis*), *C. binervis*, *C. alpicola*. The stations of these species, both of those occurring in, and of those absent from mid-Europe, are very variously scattered in Great Britain, much more so than in Germany, where they either inhabit the line of retreat of the Baltic ice from East Prussia to Holstein; or moors on the old terminal moraines, for instance in Silesia and in Upper Bavaria; or, and mainly, the moors lying in the depressions of the mountains as well as in mountain ravines, on mountain rocks, etc. (Gratformationen)[2] above the tree-limit.

The British stations fall into four main regions of the British Isles :—

1. Wales.
2. Cumberland, Westmoreland, N.W. Yorkshire, etc.
3. The Grampians from Ben Lawers northwards.
4. The scattered hill and mountain chains of West Ireland, especially round Galway Bay, in West Galway, Mayo and Sligo. It is of great interest that special species occur in each of these counties and that, as it seems to me, the species of phytogeographical interest having a distribution through all of them are very few.

[1] Vidensk. Meddel. fra den naturhist. Forening: Kjöbenhavn, 27 Jan. 188: especially p. 45.

[2] cf. W. G. Smith. "Types of British Vegetation," Chap. XII. and the literature there cited.

Of these species I select *Potentilla fruticosa*, which we saw in the station figured by R. Ll. Praeger in his " Tourist's Flora of the West of Ireland," p. 140. This station has no special orographical features : it lies south of Galway Bay, almost at sea level, in a shallow depression of the cattle pasture. There, as Praeger says, the plant is dominant:—" Generally abundant where it occurs, sometimes almost entirely usurping the ground over an acre or two, as behind Ballyvaghan," *(l.c.)*. Clare, Galway and Mayo contain the Irish Stations, the English belong to the second of the above mentioned regions. Nowhere else in the British Isles is the plant wild. Let us now compare the other European stations. The Pyrenean plant is reckoned as another species or at least a distinct race—*P. prostrata* Lap. The often cited single German station, Wemding in the North Keuper district of Bavaria may be regarded as in course of destruction or as an instance of naturalisation. In addition there are South-East Russia and Oeland. These relict stations have no connexion with each other, and since *Potentilla fruticosa* is a plant of quite different climatic conditions from the chomophytes, its occurrence throws a bright ray of light on the post-glacial development of the British flora: the species has occupied its present stations since the Baltic ice period, if not longer.

Carnarvon, in the north-west corner of Wales, is distinguished by the sole possession of *Lloydia serotina*. *Saxifraga nivalis* has here its southernmost station in the British Isles, reaching north-wards to 57·5° N. *Saxifraga rivularis* does not extend south of Ben Lawers, and ranges northwards to Westerness (57°N.) so far as I can follow the stations. *Sagina nivalis* is confined to Ben Lawers and quite a narrow area of the Scottish mountain region, *S. saxatilis* to the same region, from Ben Lawers to the north coast. These cases indicate the scattered type of distribution of the arctic-alpine plants of the British Isles. This is not, as in the Alps, a result of local endemism in the different regions combined with arctic invasion from the north, but rather a case of the colonisation of the arctic flora during the Glacial Period, the present fixed stations having been occupied at the close of the Baltic ice period. *Dryas octopetala* is one of the species which connects England, Scotland and Ireland, ranging from Carnarvon by Westmoreland to Perth and the Orkneys, and in Ireland is scattered over ten counties of Praeger's map. The habitats of this species on Black Head, south of Galway Bay, are very remarkable. At slight altitudes (100 m.) on the limestone slopes it occurs with *Euphrasia salisburgensis*,

Sesleria, Calluna, Erica and *Empetrum*. Higher up it occurs with *Rubia peregrina and Arctostaphylos Uva-ursi ;* and at 200 m., in the clefts of the hard limestone, with *Scolopendrium, Adiantum Capillus-veneris* (rare), and *Habenaria intacta* in part of its "limited and probably continuous range along the western edge of the Limestone Plain from Burren to Cong" (Praeger, *op. cit.*). I know of no similar example in the German and north Alpine Flora of so perverse a distribution and mixture of relict-stations.

The Structure of the Plant-Formations.

It appears to me natural, in all detailed work, at least on the formations of dry ground, to maintain the threefold division of the British Isles into the formations of southern and eastern England, those of Scotland, including the siliceous mountains of northern England over 250 m. (or at least over 1000 English feet), and finally those of Ireland and Cornwall.[1] Wales probably shares in the character of all three of these divisions, but we had no opportunity of seeing this highly interesting country.

It is necessary to premise that only the first of these divisions can be usefully compared with mid-Europe (Germany including the northern Alps). The north of Great Britain must be compared with Scandinavia and the Faroës, the west of Ireland and Cornwall with the north-western French peninsula (Brittany) and with the Asturias, etc.

Woodland, Scrub, etc., in Southern England.

The woods of the south and east English region show at once a striking deficiency as compared with those of the German plains and hills in the absence of *Pinus silvestris*. This tree, though very abundant on sandy soils, is not generally regarded as native in the south-east, though it was apparently general in early post-glacial times.[2] In the counties which I saw the oak and the ash, on the southern chalk the beech (with yew), and on the higher siliceous hills the birch (the oak scarcely ascends beyond 300 m.), especially *B. pubescens* (which, as compared with Germany, takes a relatively prominent position), were practically the only dominant trees, where

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[1] *Fagus silvatica* (characteristic of south-east England) is nevertheless recorded as wild in Cornwall, while in Ireland, as is well-known, it is absent.

[2] See "The Woodlands of England" by Moss, Rankin and Tansley, New Phytologist, IX, 1910. The possibility, however, of the nativity of *Pinus* in the south-east of England is there suggested, p. 134.

in Germany we should expect to see a much greater variety of both trees and shrubs. I never saw in England that delightful mixture of various trees presented by a mid-German valley traversed by a murmuring brook, where behind the alders (*Alnus glutinosa* and *A. incana*—the latter absent from England) the hornbeam (*Carpinus Betulus*) is mixed with *Acer platanoides* or *Pseudoplatanus*, *Ulmus*, *Tilia* and *Sorbus Aucuparia*, on the valley sides giving place to closed beechwoods with *Picea* and *Abies*, and making way for *Pinus silvestris* on the steeper and drier slopes. But instead, the beautiful ashwoods are highly developed in England, as I only remember to have seen them here and there on basaltic hills or in East Prussia. *Ulmus*, *Populus tremula* and *Corylus* are generally present in England as in Germany, and at higher altitudes *Sorbus Aucuparia* becomes more important. *Ilex* and *Hedera* betray the west-European influence by their abundance in the lower layers, even far to the north.

Many of the species, both of the woods, and of the open copses, scrub, and commons, which in England are known as south-western, have a very different distribution on the Continent. Two examples are *Daphne Laureola* and *Lithospermum purpureo-cœruleum*, both absent from Ireland. *D. Laureola* is distributed from Devon north-wards to York and Durham. Besides France, Aragon, North Italy and southern Switzerland, the area of these two species extends far into the south-east of Europe—Austria, Hungary, Slavonia, Herzegovina, Bosnia, Servia and southern Russia, so that many such species are reckoned in Germany as "south-eastern"! *Daphne Laureola*, however, is typically absent from the whole of Germany as far as Austria and the Swiss Jura. But other species are specifically south-western, extending from Spain to Holland and East Friesland : e.g., *Endymion nutans=Scilla non-scripta*, of whose abundance in England, even in the northern woods, we often had striking evidence.

While always bearing in mind this strong western character, even in the south-east of England, we can say, then, that the south British plant-formations, wood, low calcareous hill-flora with scrub, lowland meadows, and lowland heaths on peaty soil, are constructed very much as would be the case if low calcareous hills were present, say, in south Hanover on the edge of the north-west German moor and swamplands. I am thinking, for instance, of the scenery of South Hampshire, such as Beaulieu Heath and the beautiful beechwoods on the higher ground of the New Forest, with *Ruscus*

and *Ilex*. On the lowlying heaths, besides all the characteristic species of the western Lüneburger Heide, there are dominant *Erica Tetralix*, much *Myrica*, *Narthecium*, masses of *Hypericum Elodes*, such as would be impossible in Germany, and, on drier sands, *Erica cinerea* and *Ulex*, giving the English stamp to the vegetation. And in the same region there are the Downs, calcareous hilly country from which one sees no heath, but only ash and beechwoods, with *Sorbus Aria* and *Viburnum Lantana*, while luxuriant lianes of *Clematis Vitalba*, *Bryonia dioica* and *Tamus* climb over the scrub, the thorny *Cratægus* forms picturesque outlines on the bare hillsides, and *Conyza*, *Senecio Jacobæa* and *Cirsium acaule*, as in Germany, are characteristic herbs. But one seeks in vain for such species as *Cynanchum Vincetoxicum*, which in similar German vegetation would scarcely be absent: likewise for *Anthericum* or *Peucedanum Cervaria* in rubbly places. Thus in south-east England the mid-German hill plants make incomplete formations and the missing members are not replaced by others absent from Germany.

On the other hand, on the heaths developed on detrital sands, with *Erica cinerea* we get *Ulex europæus*, in the south *U. minor* (*nanus*), and in the west *U. Gallii*, which often take the positions that would be occupied in mid-Germany by the " dry hill-flora " [1] with a mixture of genuine steppe-plants. The hill-plants of England do not appear to be very exacting in regard to dryness, since for instance, *Geranium sanguineum* occurs in many stations on the limestone of the west coast of Ireland, mixed with *Rubia peregrina.* It is indeed commoner in the damper north and west than in the drier south-east.

THE NORTH BRITISH HILLS AND MOORS.

This flora with its numerous resemblances to that of Central Europe goes far northwards on the limestone—we botanised among it in the valleys of the Rivers Wye and Derwent in north Derbyshire—and the scenery with its bare grassy hills (about 400 m. —1200 to 1400 English feet) and ashwoods on the damper valley slopes often resembles the equally bare dolomites of the Eifel, without assuming any strongly montane character. *Helianthemum*, *Sanguisorba*, *Scabiosa*, *Geranium sanguineum*, with forms of *Rosa mollis*, are the characteristic plants, while *Sesleria cærulea* begins quite suddenly on the limestone further north (Yorkshire) beyond a barrier of siliceous rocks.

[1] cf. Drude, Hercynischer Florenbezirk (Vegetation d. Erde, 6).

The hard " grit " and the shales of the Carboniferous formation give rise to hills with slightly rounded summits to which the "Peak" of Derbyshire belongs. We visited these hills between Crowden and Greenfield and between Greenfield and Huddersfield in south-west Yorkshire and here, where the water parting between the North Sea and the Irish Sea reaches a height of only 540 m., the immense difference between the zones of vegetation and those of Central Germany become very clear. Woodland stops at an astonishingly low level : dwarf shrubs and heath, with arctic-boreal elements, and also Nardetum, begin extremely soon : on screes *Pteridium* forms a pure association in full sun and extends to a high level, till it is replaced (about 350 m.) by a new association. The flat summits are covered with widely extended peat-moors, which are not situated in depressions surrounded by ridges and peaks, as on the German mountains, but are developed on the gently rolling summits themselves. On the edges of these highlying plateaux, the moor breaks off sharply into a steep slope covered with *Vaccinium Myrtillus*, from which the rain-water flows out and collects into mountain streams. On the moor plateaux themselves the power of the water is seen in numerous rifts and channels dividing the vegetation of the " Hochmoor " into areas, from the sides of which the peat is worn away, and which form in dry weather most convenient passages between the plants of the moor scrub.

This marked depression of all altitudinal limits is without any doubt the consequence of the damp rainy climate : although the last snowfalls may take place after Easter, the snow rarely lies continuously for many weeks during winter. In Germany also we have a depression of altitudinal limits towards the damper west. The moors of the Harz, whose vegetation of Myrtilleto-Empetretum with *V. Vitis-idæa, Trichophorum cæspitosum* (=*Scirpus cæspitosus*) and *Eriophorum vaginatum* may be compared with the British, extend from 700 m. to 1080 m., but they lie in hollows which are covered with snow during the winter, or on the flat sides of the summits surrounded by woods of *Picea*. The difference of latitude from the Pennines is only 2⁰.

Of the social species of the Pennine moors, *Rubus Chamæmorus*, which forms larger masses than I have ever seen in the best East Prussian " Hochmoor," is very noteworthy. This plant only reaches a few places of the German mountain moors in the Riesengebirge, at about 1000 m.

But the absence of *Vaccinium uliginosum* appeared to me even more remarkable (*Oxycoccus* ranges from Somerset to northern Scotland). The so-called " Moorbeere " (*Vaccinium uliginosum*), which is never absent from German " Hochmoor," either on the northern plain or the mountains, which lives on the sand-dunes of the North Sea islands, and which, in the mountains from 700 m. upwards, suppresses *Vaccinium Myrtillus* and *Vitis-Idæa*, is quite absent from the south of Great Britain, occurring only from Durham and Westmoreland northward to the Orkneys. But even in Scotland, in the parts visited by us, I never saw the plant, though I was on the look-out, so that it cannot be social and abundant. It shares the distribution of *Linnæa*, and thus with that plant and *Arctostaphylos Uva-ursi* unites the second and third groups of stations of northern plants given on p. 244. *Andromeda polifolia*, on the other hand, occurs so far south as Norfolk and Somerset.

Low Altitudinal Limits of the Formations.

The altered scenery with the uncommonly low occurrence of boreal-arctic species in the mild winter climate of Great Britain is unquestionably ecologically facilitated by the damp stormy summers which have suppressed the growth of trees. In our excursions in the Pennines I saw even in deep sheltered clefts, besides weak dwarf trees of *Quercus sessiliflora* and *Betula pubescens*, only massive stems of *Sorbus Aucuparia* laden with red fruit : 100 m. higher nothing but " Hochmoor " covered the flat-topped summits and ridges. On free slopes we found as low as 250 m., between *Pteridium* and *Agrostis*, great masses of *Empetrum nigrum*. I recall that *Empetrum* occurs also on the German coast where it is exposed to damp sea-winds, and sparingly on sandstones in Saxon Switzerland at about 300 m. where damp rock clefts covered with *Sphagnum* afford a moist and cool mountain climate. But in general *Empetrum* does not occur on peat-moors below 700 m. and becomes abundant at about 1000 m., growing mostly at and above the tree-limit on free summits in the sun.

A great difference would be introduced into the physiognomy of the vegetation if *Picea excelsa* were a definite component and formed a considerable zone between the uppermost deciduous trees and the arctic-boreal associations of dwarf shrubs. In Central Europe also, if the Spruce is absent, the grass, heath and moor formations generally descend to lower altitudes. In Hercynia I recall the magnificent meadows above the beechwoods of the

basaltic summit of the Rhön ; and at the lower limit of the mountain woods in the Vosges, where dwarf communities of *Fagus silvatica* compete with mountain meadows. It appears to me certain that the Spruce spreads subspontaneously in the south of England[1], like the Sycamore and especially the Pine, and that it might become fully naturalised : it would be of great interest to try by cultivation experiments how the tree would behave on siliceous hills of more than 400 m. in height, if it were able to defy the rainy stormy British summers. One would think it could not find worse conditions than on the swampy moory slopes of the Riesengebirge at 1200 m.

THE HIGHER MOUNTAINS.

At such a height as this in Great Britain the dwarf shrub formations and the closed Nardetum has already been long super-seded by the Chomophytes, the ridge ("Grat") formation or the associations on high mountain rocks, where, between dwarf willows and mosses, rare arctic species like *Sagina nivalis* on Ben Lawers have their isolated stations.

If certain mountains in the Grampians or in Cumberland are ascended one finds first at a height of only about 250 m., surrounded by Pteridetum or Nardeto-Agrostidetum, sun-loving species such as *Saxifraga aizoides*, *Cochlearia*, *Pinguicula* and *Selaginella*, with *Chrysosplenium* in the mountain streams and round springs ; not shade-loving species like *Ranunculus aconitifolius* and *Mulgedium* in the German mountains. Only at a higher level up to about 600 m. the sides of the mountains are occupied by *Calluna*, after *Pteridium* has disappeared and given place to tufts of *Cryptogramme* at 400 m. The heaths of the mid-German mountains, on the other hand, at and above the tree limit (1000—1300 m.), attain a very strong development with *Calluna* and *Vaccinium uliginosum*, and *Calluna* alone is in Germany more dominant and more widely spread than in the British mountains which I had the opportunity of seeing.[2] From 500 to 700 m. the Nardetum, with Juncetum squarrosi, is at its strongest, and above this level *Empetrum*, *Alchemilla alpina* and *Pinguicula* begin to be so abundant that the turf has as much right to be called sub-alpine sward as the similar community of *Homogyne*, *Luzula sudetica* and *Trientalis* in the German Mittelgebirge at 1000—1200 m. A greater abundance of characteristic species naturally occurs round the cold springs : thus

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[1] I know of no evidence for this belief. [Ed. NEW PHYT.].

[2] In the Eastern Highlands of Scotland, however, Callunetum covers very wide areas on the mountain sides. Cf. "Types of British Vegetation," p. 113. [Ed. NEW PHYT.].

at 800 m. *Saxifraga stellaris*, at 900 m. *Luzula spicata* and *Sibbaldia*, at 950 m. *Carex saxatilis* (with *Bellis perennis* and *Chrysosplenium*); and above 1000 m. the pure arctic-boreal associations, are found *i.e.*, some 500 m. lower than in the Riesengebirge and Böhmerwald. On Ben Lawers *Juncus trifidus* descends to 900 m.: in corresponding places on the Riesengebirge (east slope of the Schneekoppe), where it likewise forms closed communities, only to 1420 m.

LOWLAND HEATHS.

The lowland heaths, the " heath association " or " Callunetum arenosum " of Tansley,[1] for the most part correspond with those of north-western Germany in the region of the Weser and the Ems, and on the English heaths one would often feel oneself transported to Germany if it were not for the sudden occurrence of *Erica cinerea* between *Tetralix* and *Calluna*, or of *Ulex minor* or *Gallii*, with *masses* of *Schœnus nigricans*, *Myrica Gale*, *Narthecium* and *Hypericum Elodes*, which indicate the west-European conditions. Especially striking is the purely western " Cornish heath," *Erica vagans*, on the Lizard peninsula, which is by no means a rarity, but occurs as the most important constituent of the whole heath formation in that locality. For the rest, Tansley's remark[2] that " most of the species of south-west European plants for which the Lizard district is famous occur on the grassland of the sea cliffs or in their clefts, and not on the heaths " is of great interest.

AQUATIC FORMATIONS.

The formations of water-plants, floating and submerged, the reedswamps and infra-aquatic fens, and finally the fen woods of *Alnus, Betula pubescens* and *Salix cinerea*, (with *Humulus* and *Lonicera* as lianes, and luxuriant *Osmunda regalis*) developed from reedswamp and fen, with which we became acquainted in the Norfolk Broads under the admirable leadership of Miss Marietta Pallis, are so interesting that it is impossible to pass them over. The great effectiveness of the methods pursued in England and America, which direct ecological investigation mainly to the association, and the connection or replacement, of groups of species under the stress of changing soil conditions, here became especially apparent.

It seems probable that formations corresponding with those of the Norfolk Broads, if not so variously developed or on equivalent ground, might be found in the north German plain, perhaps in the Spreewald or at Drömling. If so, a comparison would be interesting,

[1] " Types of British Vegetation," pp. 103 *et seq.*
[2] " Types," p. 110.

since it is likely that the dominant species, with the exception of a few west European ones, would be the same.

The transformation of associations, the production of "carr" (fen wood) up to the point at which *Fraxinus* and *Quercus* enter the association of bushes and trees, is still going on before our eyes, and is strikingly characteristic of the Norfolk Broads area.

In connexion with the remark in "Types" (p. 235) : "The establishment of Sphagneta and the presence of moor associations on the fen suggest that the fen association may pass into the moor-formation," I may remark on the possibility that many great "Hochmoor" regions, such as for instance that near Königsberg on the coast of East Prussia may similarly be derived from "fen."

We also had the opportunity of studying many interesting water plants, partly in communities, partly as species, and not least the famous *Eriocaulon septangulare* in Galway, one of its seven Irish stations, "ranging up the whole west coast, but avoiding the lime-stone tracts."[1]   So much has been said about the remarkable occurrence of this North American plant that I will confine myself to one remark.   The circumstance has perhaps been too much overlooked that *several* commoner or rarer species which do not belong to the circumpolar boreal floristic element, occur in both North America and West Europe, though *Eriocaulon* is the only one whose European distribution is confined to Ireland.   Thus *Lobelia Dortmanna*, which ranges as far as the Lüneburger Heide as a rarity, is distributed in the swamps of New England up to North Pennsylvania, and from Lake Superior northwards into Canada ; while an allied species, *L. paludosa*, ranges from Delaware to Florida and Louisiana.   *L. Dortmanna* is thus the species suited to a cooler climate : it strikingly avoids southern England and extends from South Wales through Cumberland to the Shetland Islands.   *Ligusticum* (*Haloscias*) *scoticum* has a similar distribution. In the New World it is distributed from the Behring Sea to Canada and Labrador : in the British Isles it occurs in five counties of the north coast of Ireland, from which it extends to northern England and Scotland.   Of water plants *Subularia aquatica* occurs in North America (Yellowstone, etc. in the west, Maine and New Hampshire in the east), and also *Isnardia palustris* and *Lysimachia thyrsiflora* : of bog-moss plants *Drosera intermedia*.   There are in fact a number of plants with interesting distributions of this sort which on this side of the Atlantic we mostly call west European, without mentioning their connexion with North America.

[1] Praeger, "Irish Topographical Botany," p. 330.

COAST FORMATIONS.

The coast formations naturally formed a very attractive feature in our studies in Great Britain, especially as the chapter (XIV) of "Types" dealing with them, and also Professor F. W. Oliver's special explanations and lists of flora relating to Blakeney on the coast of Norfolk, formed an excellent preparation for their examination. But the comparison with the German flora can be very briefly dismissed, since Germany possesses very little of interest in comparison with Great Britain, and the arrangement of the formations on the flat sandy beach of the German coast of the North Sea is poor and monotonous compared with the magnificent alternations of rocky coast, shingle-banks and extended salt-marshes, and sand-dunes with the dune hollows behind the main dunes, where *Salix repens*, just as in Belgium, plays such a noteworthy part in the association. So far as my knowledge extends, the German Baltic coast possesses only one or two species of interest which are absent from Britain, e.g., *Linaria odora*. The magnificent structure of the formations on flat or steep rocky coasts, as we saw it on the coast of Cornwall, with the stations of *Crithmum maritimum*, has its only German analogue in Heligoland. Such interesting plants as *Crambe maritima*, which ranges from the east coast of Ireland and from Cornwall to the Scottish west coast (56°N.) are only found as rarities in Holstein, Mecklenburg and Rügen. *Brassica oleracea*, which grows apparently wild on the Heligoland cliffs, is claimed with equal right as wild from Cornwall to Carnarvon. Further, England has many species, e.g., *Euphorbia Paralias* and *portlandica*, which do not occur at all on the German coasts, and also species such as *Suæda fruticosa* which exhibit plant-forms uncommon on the coasts of northern Europe. Even the meadow-like damp dune flats, which exist in the East Frisian islands, are fuller of flowers and of species in England.

Much is still left to say of the remarkable plants and their ecological relations shown to us by our kindly leaders, and of the points which struck us as visitors accustomed to formations of similar structure but of quite different floristic composition. But these remarks might easily grow into a small book and the most important points of the comparison fall into the background. Enough has been written to show how stimulating was this "I.P.E." Under its flag, which Tansley untiringly held aloft, we spent

extraordinarily instructive days, days penetrated too by the gladdest spirit of comradeship, days which we shall always remember for their strong and beautiful impressions of the world of British vegetation. I can only conclude with the hope that the pleasure which the writer of these notes himself found in the experience may find its echo in the hearts of all our British guides.

ON INDUCED VARIATIONS IN THE OSMOTIC PRESSURE AND SODIUM CHLORIDE CONTENT OF THE LEAVES OF NON-HALOPHYTES.

By Francis J. Lewis, D.Sc.

DURING an investigation into the effect of spray containing sodium chloride on the leaves of non-halophytes which is still proceeding, a series of experiments were carried out on the increase in sodium chloride content and rise of the osmotic pressure in leaves immersed in sea-water and in sodium chloride solutions.

Comparatively little attention has been given to this question during recent years. Lesage[1] experimenting with *Lepidium sativum* and *Raphanus sativus* found that sodium chloride entered the tissues of these plants with great readiness. Boodle[2] in describing the anatomical changes induced in the leaves of the wall-flower by watering with salt solutions found that such leaves gave an increased sodium and chlorine content as compared with normal leaves. The chlorine was tested by nitrate of silver, and the sodium by a flame reaction, but no quantitative results are given.

In the experiments described below all the leaves show considerable variations in weight during immersion and an increase in sodium chloride content at the end of the experiment. The osmotic pressure of the cell sap is also greater after immersion for twelve or twenty-seven hours in salt solutions than in fresh leaves on the same branch.

[1] Lesage, P. " Le chlorure de sodium dans les plantes." Comptes rendus, Tome 114, p. 143.

[2] Boodle, L. A. " Succulent leaves in the Wall-flower." NEW PHYTOLOGIST, Vol. III, p. 39.

In order to show that an increase of sodium chloride takes place in the tissues of the leaf during immersion in sea-water it was first necessary to determine the average amount of sodium chloride in the leaves of experimental plants. For this purpose leaf sections were tested with silver nitrate in the following way. Sections were cut dry and mounted directly in a $\frac{1}{10}$ gram molecular solution of silver nitrate and exposed 1-ft. from an electric lamp for twenty minutes. Leaves tested in this way after immersion in sea-water (the surface of the leaf being washed repeatedly with distilled water before the sections were cut) always showed a much greater sodium choride reaction than fresh control leaves of the same plant. The reaction was strongest in the cells of the lower and upper epidermis and the palisade layer. In all these tests the upper mesophyll cells showed the least reaction. This method does not, however, yield quantitative results, and was therefore only used as a preliminary test. A series of trials were carried out on extracts obtained by grinding up the leaves in a mortar, and making up the extract after filtration to 100 cc. with distilled water and titrating. This method was found to be unsuitable, owing to the strong colouration of the extract with chlorophyll.

The following method was then tried and found to give reliable results.

The leaves in which the amount of sodium chloride had to be determined were washed with distilled water, until the wash-water gave no opalescence with silver nitrate. The leaves were then dried in an oven at 100°C for one-and-a-half hours and weighed. They were then incinerated in an open porcelain dish at a low temperature, no redness being visible in ordinary daylight. Incineration was continued until all the carbon had been driven off, leaving a grey or white ash. According to Strecker[1] no chloride of sodium volatilizes during this method of incineration. The resulting ash was then dissolved into 100 cc. distilled water. In most cases the resulting solution was slightly alkaline, and was neutralized with a trace of pure nitric acid, phenolphthalein being used as an indicator. The solution was then titrated in the usual way with potassium chromate and a $\frac{1}{20}$ normal silver nitrate solution.

This method was used in determining the sodium chloride content of the untreated leaves in Table I and in the treated leaves in Tables II, III, IV, V and VI. The same individual plants were

[1] Strecker. *Ann. d. Chem. u. Pharm.* 54, 353.

used throughout all the experiments, and the leaves were kept in darkness between the successive weighings.

TABLE I.

Amount of NaCl contained in untreated leaves.

Plant.	Weight of leaves taken after drying for 1½ hours at 100°C.	NaCl in Ash.	.% NaCl in Ash % dry weight of leaves.
(1) *Camellia japonica* ...	... 0·7346 ...	... 0·001756 ...	... 0·2 ...
(2) ,, ,, ...	... 0·9831 ...	... 0·002960 ...	... 0·2 ...
(3) ,, ,, ...	... 3·1990 ...	... 0·007020 ...	... 0·2 ...
(1) *Ilex Aquifolium* ...	... 2·1643 ...	... 0·007020 ...	... 0·3 ...
(2) ,, ,, ...	... 0·9161 ...	... 0·005260 ...	... 0·5 ...
(3) ,, ,, ...	... 0·8477 ...	... 0·002960 ...	... 0·3 ...
(1) *Syringa vulgaris* ...	... 0·3692 ...	... 0·0029 ...	... 0·8 ...
(2) ,, ,, ...	... 0·2432 ...	... 0·0018 ...	... 0·7 ...
(3) ,, ,, ...	... 0·2482 ...	... 0·0024 ...	... 0·9 ...
(1) *Cavendishia acuminata*	... 0·6683 ...	... 0·00176 ...	... 0·2 ...
(2) ,, ,,	... 0·5088 ...	... 0·00117 ...	... 0·2 ...
(3) ,, ,,	... 0·6428 ...	... 0·00234 ...	... 0·3 ...
(1) *Arum maculatum* ...	... 0·6362 ...	... 0·00585 ...	... 0·9 ...
(2) ,, ,, ...	... 0·8673 ...	... 0·0117 ...	... 1·3 ...
(3) ,, ,, ...	... 1·3738 ...	... 0·0106 ...	... 0·8 ...

In the case of immersed leaves the following methods were used. The leaves were cut fresh from the plant and the cut end of the petiole sealed by dipping in melted paraffin wax. The leaves were cleaned with filter paper, dipped in distilled water, dried and weighed. They were then put into glass-stoppered bottles filled with sea-water or salt solution of known salinity. They were taken out, dried thoroughly with filter paper every three hours and weighed, and were then immediately replaced in the solution until the next weighing. At the end of the experiment they were washed thoroughly in distilled water until the wash water gave no opalescence with silver nitrate, and the sodium chloride determined. Three sets of leaves of each plant were taken, two sets being placed in salt solution and one set in sea-water.

Tables II and III give the results of these experiments. Only perfect leaves with uninjured epidermis were used.

TABLE II.

Variation in weight of leaves immersed in NaCl solution and in sea-water and amount of NaCl contained in leaves at the end of immersion.

I.—*CAMELLIA JAPONICA.*

Time of Weighing.	10 a.m.	1 p.m.	4 p.m.	7 p.m.	10 p.m.	1 a.m.	4 a.m.	7 a.m.	10 a.m.	1 p.m.
Weight of Leaves. Exp. 1. NaCl Solution 3·0420%	3·5042	3·4860	3·4870	3·5155	3·5964	3·6463	3·7015	3·7235	3·7745	3·8255
Exp. 2. NaCl Solution 3·0420%	1·2013	1·1982	1·1982	1·1987	1·1992	1·2034	1·2097	1·2134	1·2190	1·2205
Exp. 3. Sea-water Sol.=2·5155%	2·8998	2·8958	2·9022	2·9041	2·9156	2·9290	2·9288	2·9265	2·9300	2·9305

	Total change in weight of leaves	Change of weight expressed as % of initial weight	Weight of leaves taken for NaCl determination	Dry weight of leaves	NaCl in Ash	% NaCl on initial weight
Exp. 1	+0·3213	+9·1	3·8255	1·3606	0·0135	0·9
Exp. 2	+0·0192	+1·5	1·2205	0·4338	0·0029	0·6
Exp. 3	+0·0307	+1·4	2·9305	1·0716	0·0036	0·3

No. 1. Sections cut and placed in tap-water at 1.30 p.m. of the second day. Cells not plasmolysed except one or two in the upper mesophyll layer.

No. 2. Sections placed in sea-water at 1.30 p.m. of the second day. No palisade cells plasmolysed, but a few mesophyll cells slightly plasmolysed.

No. 3. Sections cut at 1.30 p.m. of the second day and placed in 10% NaCl solution. All mesophyll cells strongly plasmolysed. Complete recovery in 10 minutes on being placed in tap-water.

TABLE III.—*ILEX AQUIFOLIUM.*

Time of Weighing.	10 a.m.	1 p.m.	4 p.m.	7 p.m.	10 p.m.	1 a.m.	4 a.m.	7 a.m.	10 a.m.	1 p.m.
Weight of Leaves. Exp. 1. NaCl Solution = 3·0420%	2·3708	2·3975	2·4215	2·4435	2·4692	2·4746	2·4980	2·5044	2·5175	2·5325
Exp. 2. NaCl Solution = 3·0420%	4·0854	4·3073	4·4351	4·5435	4·6355	4·6968	4·7420	4·8072	4·8776	4·9338
Exp. 3. Sea-water NaCl = 2·5155%	2·7752	2·8305	2·8829	2·9525	3·0300	3·0990	3·1475	3·1755	3·2108	3·2478

	Total change in weight of leaves	Change of weight expressed as % of initial weight	Weight of leaves taken for NaCl determination	Dry weight of leaves	NaCl in Ash	% NaCl in dry weight of leaves
Exp. 1	+0·1617	+6·8	2·5325	0·9075	0·0112	1·2
Exp. 2	+0·8484	+20·7	4·9338	1·5881	0·0107	0·8
Exp. 3	+0·4726	+17·0	3·2478	1·0595	0·0094	0·9

These leaves were not tested for plasmolysis after the experiment.

Other leaves of *Ilex* have been kept in sea-water of 2·9712% NaCl for 30 hours and were then found not to be plasmolysed in this strength of solution. Subsequently they were readily plasmolysed with 10% NaCl. Other *Ilex* leaves placed for 24 hours in sea-water of 2·9712% were found to be slightly plasmolysed at the end of the experiment.

TABLE IV.—*CAVENDISHIA ACUMINATA.*

Time of Weighing.	10 a.m.	1 p.m.	4 p.m.	7 p.m.	10 p.m.	1 a.m.	4 a.m.	7 a.m.	10 a.m.
Weight of Leaves. Exp. 1. NaCl Solution=3·0420%	0·9813	0·9912	1·0057	1·0286	1·0538	1·0766	1·1002	1·1059	1·1132
Exp. 2. NaCl Solution=3·0420%	0·9546	0·9775	1·0043	1·0223	1·0421	1·0668	1·0766	1·0885	1·0876
Exp. 3. Sea-water NaCl=2·5155%	0·6294	0·6385	0·6413	0·6637	0·6885	0·7108	0·7235	0·7293	0·7308

	Total change in weight of leaves	Change in weight expressed as % of initial weight	Weight of leaves taken for NaCl determination	Dry weight of leaves	NaCl in Ash	% NaCl in dry weight of leaves
Exp. 1	... +0·1319 ...	... +12·4 ...	... 0·9169 ...	0·2415	0·0041	1·7
Exp. 2	... +0·1330 ...	... +12·2 ...	... 0·8983 ...	0·2419	0·0064	2·6
Exp. 3	... +0·1014 ...	... +16·1 ...	... 0·5416 ...	0·1443	0·0036	2·4

No. 1. No plasmolysis in sections placed in sea-water at 11 a.m. of the second day. Strongly plasmolysed in 15% NaCl solution. Complete recovery in 10 minutes on being placed in tap-water.

Nos. 2 and 3. The same as No. 1.

TABLE V.—*SYRINGA VULGARIS.*

Time of Weighing.	10 a.m.	1 p.m.	4 p.m.	7 p.m.	10 p.m.
Weight of Leaves. Exp. 1. NaCl Solution=3·0420%	0·8654	0·8346	0·8461	0·8723	0·9085
Exp. 2. NaCl Solution=3·0420%	0·8166	0·7787	0·7815	0·8043	0·8420
Exp. 3. Sea-water NaCl=2·5155%	0·7625	0·7575	0·7671	0·7772	0·8005

	Total change in weight of leaves	Change in weight expressed as % of initial weight	Weight of leaves taken for NaCl determination	Dry weight of leaves	NaCl in Ash	% NaCl in dry weight of leaves
Exp. 1	+0·0431 ...	+4·1 ...	0·6900	0·1668	0·0076	4·5
Exp. 2	+0·0254 ...	+4·3 ...	0·6100	0·1408	0·0065	4·6
Exp. 3	+0·0380 ...	+4·9 ...	0·6092	0·1360	0·0059	4·3

No. 1. Sections taken of one leaf at 11.15 a.m. Palisade cells turgid. Slight plasmolysis in a few middle mesophyll cells.

No. 2. Sections taken of one leaf at 10.45 a.m. Placed in sea-water. All cells turgid except a few upper mesophyll cells.

No. 3. One leaf taken at 10.30 a.m. Surface washed in tap-water and dried. Freshly cut end of petiole placed in tap-water. Leaf remained turgid during 48 hours and did not show any injury.

TABLE VI.—*ARUM MACULATUM.*

Time of Weighing.		9.15 a.m. 18/4/12	9.15 a.m. 19/4/12
Weight of Leaves.	Exp. 1. NaCl Solution= 3·0420%	14·1705	13·8620
	Exp. 2. NaCl Solution= 3·0420%	5·9546	5·8307
	Exp. 3. Sea-water NaCl= 2·5155%	9·0711	9·0100

	Total change in weight of leaves	Change of weight expressed as % of initial weight	Weight of leaves taken for NaCl determination	Dry weight of leaves	NaCl in Ash	% NaCl on initial dry weight
Exp. 1	−0·3085	−2·1	13·0123	0·8490	0·0715	8·4
Exp. 2	−0·1239	−2·09	5·2315	0·5242	0·0287	5·1
Exp. 3	−0·0611	−0·6	8·3712	1·1271	0·0760	6·7

No. 1. Sections cut at 9.30 a.m., 19/4/12. No plasmolysis in sea-water except in a few cells in centre of leaf. These recovered in tap-water. All cells plasmolysed with 15% NaCl.

No. 2. Leaf slightly flaccid. Cells in centre of leaf-blade obviously plasmolysed. Complete recovery when placed in tap-water.

No. 3. No plasmolysis except in a few cells in centre of leaf-blade. Recovery in tap-water. Readily plasmolysed in 15% NaCl solution.

In all cases plasmolysis and recovery extremely rapid.

All the readings in Tables II—V were carried out simultaneously at a temperature of about 12°C, with a variation of not more than 1·5°.

The figures in the Tables lead to the following general conclusions :—

1.   *Camellia japonica, Syringa vulgaris, Arum maculatum* show at first a decrease in weight both in sea-water and in salt solution of approximately the same strength.

2.   After the first 3—6 hours this decrease is succeeded by a progressive increase in weight (except in the case of *Arum*) continuing to the end of the experiment.

3.   *Ilex aquifolium, Cavendishia acuminata* show a progressive increase in weight from the time of first immersion to the end of the experiment.

4.   All the leaves experimented with show an increase in sodium chloride content, in comparison with fresh leaves of the same plant.

5.   The greatest increase in sodium chloride content is found in those leaves that are most affected by spraying with sea-water in the experiments now being carried on.   Thus in *Syringa* and and *Arum*—both strongly affected by slight spraying—the salt content increases from an average of about 1·0% to 4·5% and 8·1% respectively.   In *Ilex, Camellia* and *Cavendishia* where no wilting occurs after spraying the leaf, the salt content rises from an average 0·5%, in the fresh leaf to about ·9% in *Ilex* and *Camellia*, and to over 2·0% in *Cavendishia*.

6.   The results showing the relative variation in weight and the increase of salt content are striking.   In *Camellia, Ilex, Cavendishia*, the increase in weight must be due chiefly to the absorption of water, as the percentage increase in weight is greatly in excess of the percentage increase in salt content.   In *Syringa* and *Arum* the percentage increase in salt content is sometimes greater than the percentage increase in weight.   In *Syringa* in twelve hours the weight increased (average) 4·4%, whilst the salt-content increased (average) 3·6%.   In *Arum* the weight *decreased* (average) 2·09%, whilst the salt content *increased* (average) 5·75%.

7.   After immersion in salt solutions for twelve or twenty-seven hours all the leaves experimented with shewed an increase in the osmotic pressure of the cell sap.   Before immersion the leaf cells of all the plants were plasmolysed when placed in the sea-water or salt solutions of the strength used in the immersion

experiments, but in most cases no trace of plasmolysis was observed in leaves which had been immersed for twelve or twenty-seven hours. In the other cases only very slight plasmolysis was observed, —generally in the upper mesophyll cells. All the cells were living at the end of the experiments as they were readily plasmolysed with a 10% or 15% salt solution and quickly recovered when placed in tap water. In other words the osmotic pressure of the cell sap rises, apparently owing to the large amount of sodium chloride taken in from the solutions.

Hill[1] has lately drawn attention to the power of root hairs of some halophytes to adapt themselves to varying concentrations of salt solutions.

Miss A. C. Halket, in a recent paper[2] dealing with shoot absorption of salt-marsh plants, refers to the variation in weight in the leaves of some non-halophytes, e.g., *Primula, Tradescantia* and *Myriophyllum* when immersed in solutions of sodium chloride, and mentions that these leaves were found to decrease in weight when immersed for three to four hours.

Another point of interest is the permeability of the cell-membrane to sodium chloride as shown by the greatly increased salt content of the leaves after immersion. The phenomenon is similar to that recently described by Messrs. Moore, Roaf and Webster[3] which led the authors to the conclusion that " the varying con-
" centrations of sodium, potassium, chlorine and phosphatic ions
" within and without the cell are an expression of specific affinities
" of the definite colloids of each particular cell-type for these ions,
" and do not mean that there is a membrane acting as a closed
" gate to these ions."

[1] Hill, T. G. "Observations on the Osmotic Properties of the Root-hairs of Certain Salt-Marsh Plants." NEW PHYTOLOGIST, Vol. VIII.

[2] Halket, A. C. "Some Experiments on Absorption by the Aerial Parts of Certain Salt-Marsh Plants." NEW PHYTOLOGIST, Vol. X, p. 121.

[3] Moore, B.; Roaf, H. E.; Webster, A. " Direct Measurements of the Osmotic Pressure of Casein in Alkaline Solution." Experimental proof that apparent Impermeability of a Membrane to Ions is not due to the Properties of the Membrane but to the Colloid contained within the Membrane. Bio-Chemical Journal, Vol. VI, Part I.

NOTES ON RECENT LITERATURE.

RECENT WORK ON THE BRYOPHYTA.

SINCE the writer's series of articles on "The Inter-Relationships of the Bryophyta" appeared in this journal,[1] considerable additions have been made to the rapidly growing literature of this group. In the following notes no attempt is made to analyse, or even list, the whole of these publications, but merely to select for mention on the one hand such books and papers as appear to be of interest and importance as contributions to the morphology and phylogeny of the Bryophyta, and on the other hand to draw attention to a number of recent works dealing with the ecology of these plants. For the former object it has appeared sufficient to note only the publications of the last eighteen months, *i.e.*, new work published since the appearance of the series of articles referred to. The ecology of the Bryophyta, however, was hardly touched upon in these articles, which were concerned mainly with morphology and phylogeny, and in view of the increasing attention now paid by ecological workers to the liverworts and mosses[2] it is hoped that the bringing together in these notes of some of the scattered publications on the biological and ecological aspects of the study of Bryophyta may be of interest to students and to workers in this field. Were the object in view that of noting every recent addition to the knowledge of the Bryophyta, it would be necessary to indicate some hundreds of publications, but the limited scope of this article will account for the absence of references to the greater part of the floristic literature and to cytological and physiological investigations in which the spores, antherozoids, etc., of Bryophyta were used as materials.

Leitgeb ("Untersuchungen über die Lebermoose," 1874-1881) described the air-chambers of the Marchantiales as arising by the outgrowth and division of the superficial cells of the upper side of the thallus. Until recently this explanation has been generally accepted, being repeated not only in compilations but in original memoirs dealing with the subject. In 1907, however, Barnes and Land (*Bot. Gaz.*, Vol. 44) investigated the development of the thallus in some of the higher Marchantiales, and concluded that the chambers arise by splitting of the cell-walls in the upper tissue of the thallus, their origin being schizogenous like that of the air-chambers in the parenchyma of vascular plants. These authors did not examine any of the lower Marchantiales (Ricciaceæ, etc.), but suggested that the chambers of all the Marchantiales probably arise by a similar process of splitting of the internal walls. They also claimed to have traced each chamber in the higher genera to a single mother-cell. In 1910 Miss Hirsch (*Bull. Torrey Bot. Club*, Vol. 37) examined a number of species of *Riccia*, and found that the explanation given by Barnes and Land apparently held good for *Riccia natans* and *R. fluitans*, but that in other species of *Riccia* the

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[1] NEW PHYTOLOGIST, Vol. IX (1910) and Vol. X (1911); also issued as "NEW PHYTOLOGIST Reprint No. 4."

[2] See, for instance, "Types of British Vegetation" (Cambridge, 1911).

deep narrow chambers arose according to the method described by Leitgeb. In reviewing this paper, Land (*Bot. Gaz.*, Vol. 49, 1910, p. 393) rightly pointed out that the authoress had not produced conclusive evidence either way, and that " such investigations should be preceded by a careful study of the development of the thallus from the growing-point, and there should be a clear conception of the arrangement of the cells which result from this growing-point." Petsch (31) has now made a thorough investigation of the air-chambers of the Ricciaceæ, and has traced carefully the fate of the dorsal segments cut from the initial-cells of the growing-point. His descriptions and figures leave little doubt that the interpretation given by Barnes and Land applies to the whole of the Marchantiales—in all cases the chambers arise by splitting of cell-walls in originally compact tissue. In the simpler species of *Riccia*, this splitting occurs at a relatively late stage, and but little lateral expansion of the thallus occurs afterwards, hence the chambers form simply deep narrow vertical canals ; but in *Riccia fluitans*, as in the majority of higher Marchantiales, the splitting stops short of the uppermost layer, and expansion occurs, so that the chambers become widened laterally ; finally, in *Riccia natans*, as in some of the higher forms (Operculatæ and *Bucegia*), the splitting process is confined to certain portions at different depths from the surface, the result being a network of chambers forming a mass of spongy tissue. The writer has re-examined microtome preparations of various Marchantiales, and can confirm the accounts given by Barnes and Land and by Petsch, as to the schizogenous origin of the chambers, but cannot follow the former in referring each chamber in *Marchantia*, etc., to a single mother-cell. According to the diagram given by these authors, each chamber should, on their view, be separated from its neighbours by a double layer of cells ; but as a matter of fact these vertical partitions are usually only *one* cell in thickness.

In the genus *Riccia* three types of air-chambers may be distinguished—(1) narrow canals bounded by four cell-rows, as in *Riccia glauca*, etc. ; (2) wider canals bounded by about eight cell-rows, as in *R. vesiculosa* ; (3) wide chambers separated by lamellæ, as in *R. fluitans* and the other species belonging to the section or sub-genus *Ricciella*. Juel (16) has shown that in *R. Bischoffii* the thicker median portion of the thallus shows air canals of the first (*Euriccia*) type, but in the thinner lateral wings of the thallus the chambers are wide and separated by lamellæ, while between the " midrib " and the " wings " there are transitional chambers resembling those of *R. vesiculosa*. The differences between the three types are simply due to differences in rate and direction of growth of the tissues in the various regions of the thallus subsequent to the splitting by which the chambers are laid down in the first instance. The existence of transitions between the " Euriccia " and the " Ricciella " types makes it unnecessary to maintain the division of the genus *Riccia* into two or more sub-genera, which some writers have even raised to the rank of genera.

Nicholson (27), in an admirable account of the Hepaticæ of Sussex, records some interesting details concerning the morphology of various species of *Riccia* which he has observed in the field and cultivated indoors. His observations make it extremely probable

that in the classification of this genus far too much stress has been laid by systematists upon the presence or absence of hairs and violet colouring in the thallus—"features which are very much controlled by the amount of exposure to light and drought which the plant experiences." On the other hand, he emphasizes the comparative constancy of the form of the thallus in transverse section.

Massalongo (24) has published an excellent account of the European Ricciaceæ, with new and admirable figures of the great majority of the species; this memoir forms a welcome supplement to the literature of an important and somewhat difficult family, and in various respects amplifies the recent treatment of the Ricciaceæ by Müller in the new edition of Rabenhorst's " Kryptogamenflora."

Meyer (25) has described in detail the embryology of *Corsinia*, an interesting genus which is in many respects a connecting-link between the Ricciaceæ and the higher Marchantiales. His observations on the development and division of the spores agree with those described for *Riccia* by Beer (*Ann. Bot.*, Vol. 20, 1906) and by Lewis (*Bot. Gaz.*, Vol. 41, 1906); the x and $2x$ chromosome-numbers are apparently 11 and 22. The early development of the sporogonium shows an octant-stage, as in the majority of Marchantiales, and the separation of the one-layered capsule-wall from the central tissue (archesporium) occurs at a very early stage, while the differentiation of the fertile cells (spore-mother-cells) from the sterile cells (" rudimentary elaters") of the archesporium is relatively late. The sterile cells for a considerable time form a connected network with spaces in which lie the developing spores, but later these cells separate and, after having been depleted of the greater part of their contents to nourish the spore-mother-cells, again become filled with starch-grains. This paper adds *Corsinia* to the small list of Bryophytes whose life-history is now known with tolerable completeness.

The same author (26) describes a number of abnormalities observed in the sexual organs of *Corsinia*, and discusses these, with other more or less similar cases recorded in recent years in various Bryophytes, in reference to their bearing upon the phylogeny of the archegonium. He lays stress upon these abnormalities as furnishing support for the views of Davis, Goebel, Schenck, Hallier, Potonié, and others, regarding the origin of the archegonium from an organ like the " plurilocular sporangium " of the Brown Algæ.[1]

Deutsch (5) has cleared up some doubtful points in the structure of *Targionia hypophylla*, and contributed some interesting remarks on the classification of the Marchantiales. He finds that the thallus grows by a single apical cell, and that the involucre around the archegonial group is complete and well-developed before the archegonia are fertilised. The present writer has preparations which confirm Deutsch's observations on these two points, but cannot agree with Deutsch as to the absence of a rudimentary " elaterophore "(represented, it is true, only by a few short spirally thickened cells attached distally to the inner surface of the capsule) or as to the absence of lobing in the spore-mother-cells. Deutsch sets forth an ingenious method for estimating the systematic values of various characters of gametophyte and sporophyte in the classi-

[1] See Review of Schenck's paper, in NEW PHYTOLOGIST, Vol. VIII, 1909, p. 234.

fication of the Marchantiales, and concludes that *Targionia* and *Cyathodium* are not closely related, the affinities of the latter being more probably with the Corsiniaceæ.

Schiffner (36) has described in some detail the morphology of *Noteroclada*, a monotypic South American genus until now very incompletely known. The author amplifies and corrects in various respects the earlier descriptions of this interesting plant, which though belonging to the Anacrogynous Jungermanniaccæ shows differentiation into a somewhat broad stem and two rows of leaves. The sexual organs are produced on the upper side of the stem, the archegonia along the middle and the antheridia in lateral rows on either side. The antheridia are sunk in pits, as in *Pellia*, and the antherozoids are unusually large. The fertilised archegonium is surrounded by a single envelope ("perianth"); the haustorium ("foot") of the sporogonium is produced into a sheath ("involucellum") around the base of the seta; the inner layer of the capsule-wall has well-developed spiral fibres. Schiffner concludes that *Noteroclada* is closely allied to *Treubia* and connects that genus through *Petalophyllum* to *Fossombronia*. The family to which these genera, together with *Pellia* and *Blasia*, belong (Codoniaceæ) is one of the most interesting among the Hepaticæ, as it illustrates in a remarkably complete manner the evolution of the leafy shoot from the simple thallus.

Several interesting additions have recently been made to the knowledge of the familiar liverwort *Pellia epiphylla*. Miss Greenwood (13) has published the results of microtoming *Pellia* material collected at frequent intervals throughout the year, but has not added materially to previous knowledge of the morphology of this plant; her technique appears to have been good, however, and her description of this at the beginning of the paper may be useful to workers taking up the study of liverworts, which present some difficulties as regards micro-technical methods. That even the most extensively studied of "type" plants may yield interesting results upon renewed investigation is well illustrated in the case of *Pellia* by the recent papers of Wallis and of Lesage. Wallis (44) has described, for the first time, the curious method by which the opening of the ripe capsule takes place along the special dehiscence-lines (laid down at a fairly early stage in development, and found in various other liverworts, though rarely so conspicuous as in *Pellia*)—"the dehiscence begins equatorially in two only of the lines, and the splits gradually extend to the poles till the capsule opens in two hemispherical portions; a split then begins to appear in the middle of the back of each of these hemispheres along the other dehiscence lines, eventually dividing each hemisphere into two longitudinally, and so forming the four capsule valves." The writer has this spring fully confirmed the account given by Wallis; probably this peculiar mode of dehiscence serves to prevent the premature falling-out of spores, before the hygroscopic elaterophore has been exposed to the air long enough to spread out and fulfil its function of bringing about gradual spore dispersal.

Lesage (18), in a series of short but interesting notes on *Pellia*, describes his observation of "polyembryony," or more acurately the formation of two fully-developed sporogonia from different archegonia in the same involucre, a somewhat rare occurrence (though

frequently several archegonia in an involucre may be fertilised and embryo-formation proceed to a certain point in each) which leads Lesage to make interesting comparisons between the Junger-manniales with their single long-stalked sporogonium and the higher Marchantiales in which there are several sessile or shortly-stalked sporogonia carried up on the carpocephalum (archegoniophore) ; the results of isolating nearly mature but still sessile sporogonia from the gametophyte and placing them in water—the detached sporo-gonia showed normal elongation of the seta and dehiscence of the capsule ; experiments with reference to the influence of stage of development, temperature, presence of the calyptra, and other conditions upon the rate of elongation of the seta.

Fräulein Lilienfeld (19) describes some new features in the morphology and biology of *Haplomitrium Hookeri*, of which she was fortunate enough to find large quantities on the banks of a small lake in the Carpathians. She finds, for instance, that every transition occurs between the rhizome and the erect green leafy shoots, the latter showing in feeble light great reduction of the leaves ; the tips of the rhizomes bear numerous mucilage papillæ, so crowded as to form a pseudoparenchyma comparable in function with a root-cap. Several parasitic and saprophytic fungi, as well as endophytic algæ, occur in the cells of the rhizome ; a new fungus species, *Pythium Haplomitrii*, is described. The capsule opens by a single longitudinal slit ; the antheridia are arranged all round the stem, chiefly in the axils of the leaves.

Evans (7) has described in detail the methods of branching in the Acrogynæ, distinguished by the position and age of the segment (cut from the apical cell of the shoot) from which the branch arises and by the portion of the segment which is devoted to the formation of the branch. In terminal (apical) branching, phylogenetic and ontogenetic considerations indicate that the primitive type is that in which the entire half of a segment is used up to form a branch, the other types arising from this by restriction of the portion of segment used up ; intercalary branching doubtless came later, and is correlated with comparatively feeble growth of the shoot.

Schiffner (37), in an extremely interesting revision of the species of *Chiloscyphus* found in Europe, North America, and northern Asia, clears up various hitherto doubtful points in the morphology and taxonomy of this genus, and discusses the influence of various environmental factors upon the form and structure of the more polymorphic species. Forms growing on a substratum rich in lime are characterised by great enlargement of the leaf-cells as compared with varieties found on lime-free substrata ; an aquatic mode of life is accompanied by sterility, as is usual in other liverworts, but in this genus the development of archegonia appears to demand drier conditions than in the case of other sub-aquatic Bryophyta ; plants growing in cold running waters are distinguished by small size of the leaves and leaf-cells, as compared with the large-leaved and large-celled varieties found in stagnant waters, though apparently these differences are not due simply to the higher summer temperature of stagnant as compared with running water, since forms growing in high and exposed moorland pools with low summer temperature are usually dwarfed in size of leaves and cells. In a paper on the Ptilidiaceæ, Schiffner (35) gives some

interesting new observations on the arrangement of the antheridia, in which characteristic and constant differences occur between the different genera; he also correlates the structural and habitats of the various members of this interesting family, which though small includes forms ranging from aquatics to extreme xerophytes.

Two interesting new genera of Jungermanniales have been recently described—*Trichocoleopsis* (Ptilidiaceæ) by Okamura (28) and *Goebeliella* (Lejeuneaceæ) by Stephani (41). The genus *Trichocoleopsis* agrees with Trichocolea in having no perianth, but also shows affinities with *Mastigophora, Ptilidium,* and *Lepidolaena* (*Polyotus*), and is an interesting link between these three genera on one hand and the somewhat isolated genus *Trichocolea* on the other. The genus *Goebeliella* is apparently allied to *Frullania*, but instead of the usual saccate lobule and stylus each leaf has a pair of similar lanceolate outgrowths; these may either represent a split lobule without a stylus, or one may be a rudimentary lobule (like that normally present in the genus *Jubula*) and the other a well-developed stylus. In any case the new genus appears to the present writer to form an interesting transitional form between *Frullania* and *Jubula* ; it differs markedly from *Frullania* in the form of the perianth, which is smooth and truncated with a wide mouth.

Buch (3), in a paper on the production of gemmæ in Hepaticæ in general, has described a case of endogenous development of gemmæ in *Haplozia cæspiticia*, the details being similar to those described for *Metzgeria* by Evans (*Ann. Bot.,* Vol. 24, 1910) and for *Aneura* by various writers. In the great majority of liverworts, the gemmæ arise by exogenous development, cases of endogenous origin being known only in these three genera. The gemmæ are in most cases small and few-celled, arising from the leaves or stem or both, usually in clusters, in the region of the growing-point, and their formation is often associated with limitation of growth, the entire growing-point being frequently given over to their production; but the production of discoid gemmæ, found in a small number of genera (mostly epiphytic forms), rarely affects the growth of the plant to any marked degree. The development of these discoid gemmæ has recently been described in detail by Stevens (42) in species of *Coleolejeunea* and *Radula*; by Evans (6) in species of *Coleolejeunea, Leptocolea,* and *Aphanolejeunea* ; and by Goebel (10) in a tropical epiphyllous species of *Radula*, in which the gemmæ attain a remarkable size, being larger than the leaves that produced them, before being set free.

Garjeanne (8) has studied in detail the infection of various leafy liverworts by the fungi which produce mycorhiza. In some cases the entrance of the fungus hyphæ appears to cause thickening of the walls of the rhizoids, and a kind of gall may be produced by the swelling up of the tip of the rhizoid which becomes filled with coiled hyphæ. The hyphæ appear to belong to several distinct fungi, but the commonest proved, on isolation and culture, to be a new species of *Mucor (M. rhizophilus),* closely related to *Mucor racemosus*. In cultures, infection with the fungus usually caused the death of the plant, but in nature the fungus rarely if ever has any ill-effect and the association is doubtless symbiotic. Garjeanne suggests that the fungi filling the rhizoids may serve mechanically promoting in the absorption of water and salts from the substratum.

Before proceeding to the consideration of the literature on the morphology and biology of the Musci, and on the ecology of Bryophyta in general, mention may be made of some of the more extensive works recently published in Systematic Bryology. The first volume of Muller's section on the Hepaticæ in the new edition of Rabenhorst's " Kryptogamenflora " has recently appeared; when completed, this will undoubtedly be the best general account of the European liverworts, containing descriptions and (in most cases) figures of the species, while greater attention is given to biology and phylogeny than in any previous floristic work of equal scope on these plants. Other systematic publications still in progress are Stephani's great work on the Hepaticæ, in which are given diagnoses of all the known species of the world ; Schiffner's invaluable series of exsiccata of European liverworts, with the accompanying critical descriptions; Roth's truly stupendous attempt to describe and figure in detail from actual specimens all the known species of mosses, as a sequel to his similar work on the European species ; and various moss exsiccata which are being issued. Of special importance to British students of Hepaticæ is the appearance of Macvicar's systematic work (23), which has just been published, containing descriptions and figures of all the species of Hepaticæ found in the British Isles ; a review of this important work will appear later in these columns.

One of the most important systematic bryological works of recent years is that of Warnstorf (45) on the Sphagnaceæ. This great work, which has occupied the author for six years and which is the fruit of his long labours on this difficult and important genus, is divided into a general part and a special part. In the former, there is given an account of the progress of sphagnology during the last century, with an extensive bibliography, followed by a general account of the morphology, biology, and geographical distribution of the peat-mosses. In the special (systematic) part the whole of the known species (350 in number) of *Sphagnum* are described, with figures of leaf and leaf-sections in practically every case ; with very few exceptions the author of this great monograph has examined all the species described. This work is of fundamental importance, not only for specialists in bryology but also for workers on the ecology of areas where the peat-mosses form a conspicuous element in the vegetation. It is not to be expected that all systematists will agree with the details of Warnstorf's classification, which has been subjected to severe criticism by Röll and other writers. One of his recent critics (1) points out that Warnstorf is frequently led into error through insufficient consideration of the work of other botanists and unreliability in observations involving minute details, but such lapses do not to any serious extent detract from the value of his latest and greatest work nor from his claim to rank as the leading authority on the Sphagna.

The phylogeny of the Musci has recently been discussed in an important work by Loeske (20), which is devoted to criticism of the methods and schemes of classification hitherto adopted by systematic bryologists. Loeske's book, which is indispensable to all students of the Musci and of Bryophyta in general, is likely to exert great influence on future work in this field. The author's own researches have shown that in many cases, especially among Sphagna and aquatic Hypnaceæ, mere habitat forms have been described as

distinct species, that various species and even genera are clearly artificial and include "biological" forms of remote affinity, and so on. He lays stress on the importance of taking into consideration the biology and ecology as well as the morphology of the Musci, in order to arrive at something approaching a natural system of classification. Though Loeske does not put forward a new scheme of classification of the Musci, regarding this course as premature until further work has been done, his views in this matter agree closely with those of Fleischer and Lorch, which were followed by the present writer in his recent attempt to formulate a new classification of the Bryophyta.[1]

Lorch (21) has supplemented his fine monograph of the Polytrichaceæ by a detailed paper on the structure and mechanism of the tissues concerned in the " hygroscopic " movements of the leaves in this family of mosses.

Passing by various papers in which the spores, etc., of mosses were used as materials in physiological and cytological researches, there remain for mention several publications of interest concerning the biology of these plants and their adaptations to the varying conditions of their habitats. For instance, Schoenau (38) has investigated the methods of branching in mosses, with special reference to the influence of external conditions, and has demonstrated the marked influence of light and of moisture in particular upon the occurrence and form of branching; while Janzen (17), in an interesting paper which may be said to break new ground so far as bryophytes are concerned, has described the modes of branching and leaf-arrangement in various liverworts and mosses from the point of view of " leaf mosaic " adaptations.

Irmscher (15) has investigated experimentally the resistance of cold and drought by mosses, and finds that while most of the species used showed great powers of resistance to continued desiccation, they were readily injured by alternate desiccation and soaking at short intervals; the dormant axillary buds are much more resistant to drought and cold than are the leaves; and that mosses of the most diverse habitats show a striking uniformity in regard to cold resistance, though varying greatly in their resistance to desiccation. Grebe (12) has published an extremely interesting and well-arranged account of the various structural adaptations of xerophilous mosses. Such adaptations in the sporophyte (sporogonium) include absence or shortness of the seta, causing the capsule to be sessile or nearly so, and thus enveloped by the uppermost leaves of the gametophyte; downward curvature of the seta, causing the young capsule to be plunged among the leaves— later, the seta becomes erect, to facilitate spore-dispersal by the censer-mechanism of the ripe capsule : the presence of a large or inflated calyptra which completely envelops the capsule, or of a hair-clad calyptra as in Polytrichaceæ; sheltered position of the stomata, which occur in the grooves of the furrowed capsules of *Orthotrichum*, and in the annular depression between capsule and apophysis in *Polytrichum*, and so on. Xerophilous adaptations in the gametopyte include the common cushion-like habit of the plants; hayaline hair-points on the leaves; leaves with broad midrib and narrow lamina; more or less completely rolled-up leaves;

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[1] New Phytologist, Vol. X (1911), pp. 29-43.

curved and sickle-shaped (falcato-secund) leaves; sheathing leaf-bases; papillæ and mamillæ—solid and hollow outgrowths respectively of the leaf-cells; water-storing tissue in the leaves; thick-walled leaf-cells; increase in number of layers in the lamina to two or more; strengthening of the leaf-margin by increase in number of cell-layers; development of lamellæ and other outgrowths on the surface of the leaf; undulation, wrinkling, and folding of the leaf; presence of paraphylls and dense rhizoid-covering on the stem; hygroscopic movements of the leaves, and so on.

Space does not permit detailed notices of a number of recent floristic works on Bryophyta which are of interest on account of the greater attention which is now being paid by systematic writers to observations on the biology and ecology of these plants. Increasing numbers of systematic bryologists are bringing to bear upon the problems of relationship the results of recent microscopic and physiological work, and realising the importance of studying bryophytes season after season in the field in order to observe the influence of changing conditions of light and moisture and other factors on the morphology of these plants. On the other hand, workers in Ecology are realising, to a greater extent than formerly, the important part played by bryophytes as dominant, associate, or pioneer plants in the vegetation of arctic-alpine, cliff, heath and moorland formations.

The ecological importance of the genus *Sphagnum* has, as might be expected from the conspicuous rôle played by these mosses in heath and moorland bogs, given rise to a considerable literature. During the last few years new ground has been broken as the result of biochemical researches on peat and the peat-mosses (Sphagnaceæ), opening up a line of work which has already yielded important results. The first detailed work in this direction was that of Czapek (Flora, Band 86, 1899), who found that the cell-walls of *Sphagnum* and other aquatic mosses contain an antiseptic phenol-like substance which he named " sphagnol," also that the membranes in *Sphagnum* are rich in pectic bodies. In two papers devoted to the question of the calciphobous character of *Sphagnum*, Paul (29, 30) found that not all salts of calcium have an equally injurious effect; that the most injurious are the alkaline salts of this metal, *e.g.* calcium carbonate, and of potassium and sodium, and free alkalis; that the peat-mosses give an acid reaction, suggesting that the injurious effect of calcium carbonate is perhaps due to the neutralisation of the acid; that, as Gully had shown, high-moor species contain more acid than low-moor species, the former being more sensitive to lime; that on high moors there is less mineral food available in the substratum for the Sphagna and the plants take more food from the air, the acids probably playing an important part in this process; that the amount of acid and the degree of sensitiveness to their neutralisation decrease as the amount of available mineral food increases. The more recent work of Baumann and Gully (2) has overthrown the old views concerning the existence of free " humic acids " in peat and the peat-mosses, and has shown that the acid reaction of peat and of living *Sphagnum* plants is due not to true acids but to colloidal substances of acid character which are present in the walls of the hyaline leaf-cells, and are doubtless identical with the pectin-like substances extracted

from *Sphagnum* by Czapek. These authors give elaborate chemical data regarding the adsorption of bases and acids by these *Sphagnum* colloids from solutions of various salts, showing conclusively that they agree with other colloids in their behaviour, and that the properties of peat and humus are to be interpreted as colloid and adsorption phenomena according to the laws regulating the relations of colloids to other substances. It may be noted, however, that Baumann and Gully's conclusions have been challenged by Tacke and Süchting (43) in a recent paper, in which the authors contend that there is insufficient evidence of the existence of special " peat colloids " or the non-existence of " humic acids."

Among works devoted to Bryophyta, and more general publications, in which these plants are treated from the ecological point of view, mention may be made of recent papers by Macvicar (22), Grebe (11), Györffy (14), Spindler (40), Smith (39), Crampton (4), Rübel (32), Giesenhagen (9), and Sapehin (33).

Of such publications, two may be selected for summarising here, on account of the comprehensive and detailed manner in which the authors have treated the ecology of Bryophyta. The best general account of the subject that has yet appeared in this country is Wheldon's recent work (46), in which he describes a number of the more striking " social moss groups," *e.g.*, those dominated by *Rhacomitrium lanuginosum*, *Sphagnum*, the " harpidioid " Hypnaceæ, the interesting succession of bryophyte associations on sand-dunes, and the arctic-alpine *Marsupella* association. Schade (34), on the other hand, has published what may be described as the first result of the application of detailed or " intensive " ecological methods to the study of Bryophyta; that is to say, he has selected a relatively small area and made a minute and thorough study of the bryophytic flora and of the correlation between this and the various conditions of the habitat, with exact observations and measurements of the physical factors. Schade deals with the bryophytic vegetation (with some references also to the lichens, fungi, and algæ) of rock-surfaces in the mountains of Saxony; the phanerogamic plant-geography of this region has been already worked at by Drude (on whose suggestion Schade began his research) and other ecologists. Schade distinguishes three main types of habitat—moist, flooded, and dry rock-surfaces. To the moist (*bergfeuchte*) type belong nearly all rocks with northern aspect; the surface is uniformly moist but not dripping. Such rocks show several distinct facies, the lowest, wettest, and most deeply shaded being characterised as the *Pellia* facies, with *Pellia epiphylla* as dominant form. Higher up comes the *Conocephalus* facies, with *Conocephalus* (*Fegatella*) *conicus* dominant; other bryophytes, growing in the spaces between the thallus-branches of this liverwort, rarely produce sporogonia in this facies. Other facies in this moist type are characterised respectively by *Calypogeia* (*Kantia*) *trichomanis*, *Diplophyllum albicans*, *Leptoscyphus Taylori*, *Rhabdoweisia fugax*, *Dicranella heteromalla* and *D. cerviculata*, *Tetraphis pellucida*, and *Odontoschisma denudatum* ; while various lichens are dominant forms in other facies. The author describes the general conditions of each of these facies, with notes on the dominant and associate species in each. The cryptogamic vegetation of the dripping (*überrieselte*) rocks shows three facies, characterised by diatoms, green algæ, and the liverwort

Haplozia sphærocarpa, the latter accompanied by other hygrophilous bryophytes. On dry rocks, chiefly with southern exposure, the cryptogamic flora shows two facies, one dominated by the lichen *Calicium chlorinum,* the other by species of *Gyrophora* and other lichen genera, accompanied by a few bryophytes. Schade gives detailed results of his observations on the various factors of the habitats described—light, air temperature, soil temperature, temperature inside the patches of bryophytes and lichens, relative humidity, evaporation, water content of the rock-surface, etc. The internal temperature of the moss- and liverwort-patches is intermediate between the temperature of the substratum and that of the air ; in shaded places it is always below the latter, in sunny places always higher. In summer this internal temperature is higher than the soil temperature ; in winter it is lower than the soil temperature but higher than the air temperature.

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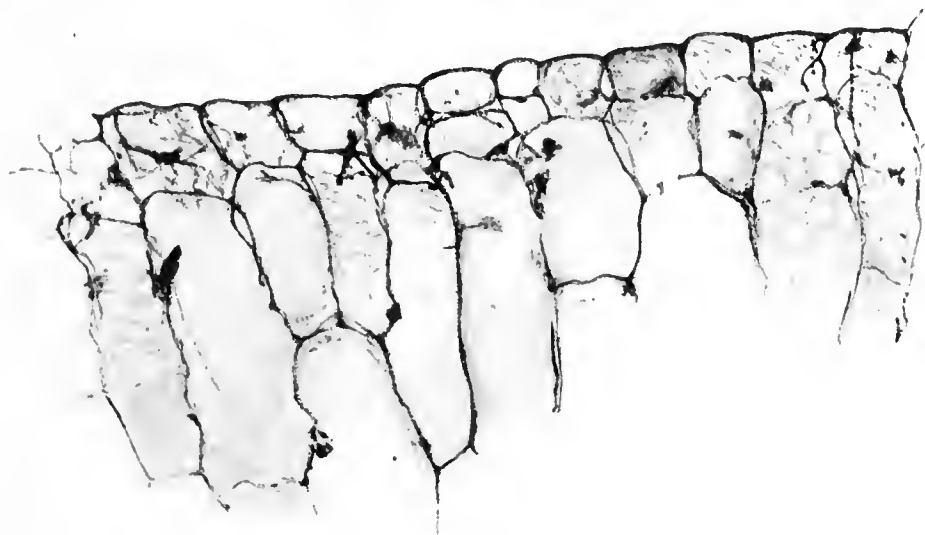
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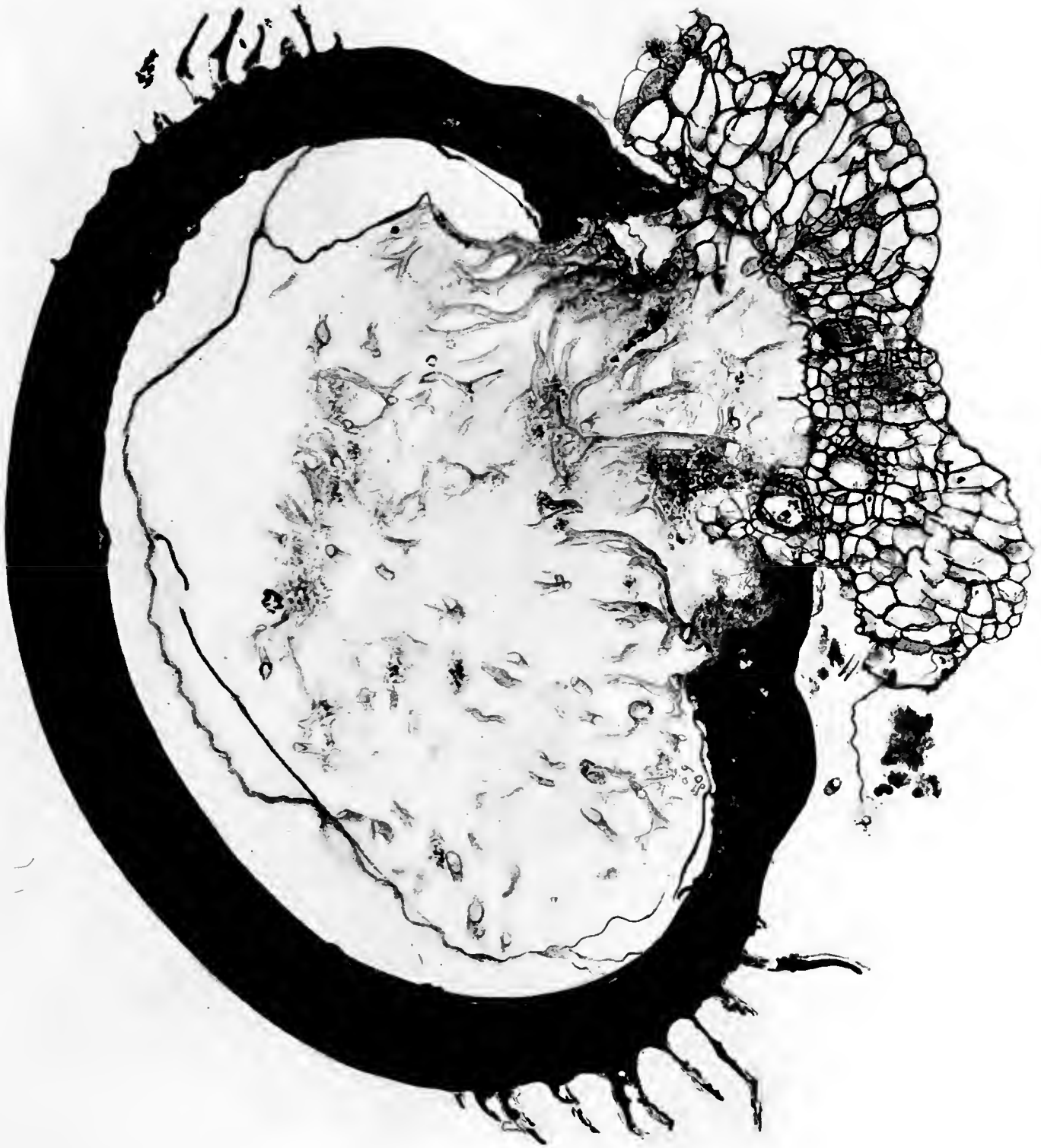
M^C LEAN - BOTHRODENDRON.

EINIGE VERGLEICHE ZWISCHEN BRITISCHER UND SCHWEIZERISCHER VEGETATION.

VON C. SCHRÖTER.

ZUNÄCHST schliesse ich mich aus vollem Herzen all den dankenden und lobenden Aussprüchen der übrigen " Foreign members " der internationalen Phytogeographischen Exkursion über die unvergesslichen Tage an, die wir der Gastfreundschaft unserer britischen Freunde zu verdanken hatten.

Sie waren eminent fördernd für uns, diese Tage, durch die dargebotene grosse Summe wissenschaftlicher Erfahrungen und Diskussionen über pflanzengeographische Begriffe, anregend durch die vorbildliche Art, in welcher die britische Phytogeographie arbeitet, reich durch die ununterbrochene Serie interessanter Vegetationen und schöner landschaftlicher Szenerien, und herzerquickend durch die Freundschaft sympathischer Kollegen.

Die vorausgehenden Erörterungen meiner kontinentalen und amerikanischen Mitgäste haben fast alles schon gestreift, was ich von besonders interessanten Erscheinungen zu sagen hätte. Ich muss mich deshalb auf ganz wenige Punkte allgemeiner Natur beschränken.

1. Die Organisation des Phytogeographischen " Survey " in Grossbritannien hat meine Bewunderung, besonders durch folgende Momente Lerregt: die eitung durch ein Comité, die eine einheiteliche Gestaltung verbürgt; die rasche und erfolgreiche Anhandnahme der " primären " kartographischen Darstellungen in 1 : 63360, basiert auf eine vorausgegangene Einigung über Nomenklatur und Farbengebung; die grosse Zahl junger, enthusiastisch arbeitender Männer die nun zum Teil schon die eingehendere Detailarbeit

in grösserem Masstab unternehmen ; das freundschaftliche Zusammenwirken aller Kräfte und endlich, "last not least," die geistige Beweglichkeit der englischen Botaniker, die es mit sich brachte, dass eine ganze Anzahl vorher auf andern Gebieten in hervorragender Weise tätiger Gelehrter sich der aufblühenden Richtung zuwandte. Dadurch wurde eine Menge neuer, insbesondere physiologischer Gesichtspunkte in die Pflanzengeographie hineingetragen, und so kam in überraschend kurzer Zeit eine bedeutende Summe phytogeographischer Ergebnisse zu Stande.

Das dabei die von Clements und Cowles in unsere Wissenschaft eingeführte dynamische Fragestellung in hervorragender Weise als Leitmotiv diente, macht diese Ergebnisse für uns Kontinentale besonders lehrreich, da bei uns diese Fragen erst gestreift wurden.

Die schönen phytogeographischen Arbeiten des auch botanisch geschulten schottischen Geologen Crampton zeigen deutlich, wie notwendig und fruchtbar für diese Richtung umgekehrt eine tüchtige geologische Schulung des Phytogeographen sein muss.

In all' diesen Dingen können wir Kontinentalen vieles von unsern britischen Kollegen lernen !

2. Mit Bezug auf die Vegetation möchte ich zunächst einige Punkte im Vergleich mit unserem schweizerischen Mittellande zwischen Alpen und Jura streifen, das als regenreiches Laubholzgebiet am ehesten sich mit Grossbritannien und namentlich mit England im engeren Sinne vergleichen lässt.

Ganz auffallend ist der Unterschied in der *anthropogenen Umformung* der Vegetation, in dem Einflusse des Menschen auf die Pflanzendecke, in England einerseits, in der Schweiz anderseits. Betrachten wir zunächst die Wälder.

In Grossbritannien wie in der Schweiz haben wir im unterhalb der Baumgrenze liegenden Gebiete ein ausgesprochenes Gehölzklima ; es ist also der Wald seit der Herrschaft der jetzigen Bedingungen die klimatische " Klimaxformation."

Wald*frei* waren in Grossbritannien (nach Tansley) nur : Die salzhaltigen Böden und Strandwälle (shingle beaches) der Meeresküste, die Wanderdünen, wahrscheinlich manche arme Kalkböden mit primärem Grasland (so z.B. auf den " Downs "), wahrscheinlich auch manche arme Sandböden mit primärer Heide, die Rohrsümpfe, und Hochmoore, die Schotterbänke der Flüsse.

Wald*frei* waren im schweizerischen Mittelland zwischen Jura und Alpen : die Moore zum Teil, die Rohrsümpfe der Seeufer, die

vom prähistorischen Menschen besiedelten und durch ihn waldfrei gehaltenen steppenähnlichen Flächen,[1] zu steile Hänge, die Schotter der Flussalluvionen und Bachschuttkegel.

In beiden Ländern räumte der Mensch mit den ursprünglichen Wäldern gewaltig auf: im schweizerischen Mittelland macht gegenwärtig der Wald nur noch 21% der Gesamtfläche aus (nach Coaz, 1888); in Grossbritannien wurde die Bewaldung herabgedrückt auf 1·5% (Irland), 3·9% (Wales), 4·6% (Schottland) und 5·3% (England); es gehört zu den waldärmsten Ländern Europas. In beiden Ländern sind Gebüsche, Aecker, Wiesen, Streurieder und Weiden, in der Schweiz auch Rebgelände, in Grossbritannien ausserdem der grössere Teil des Heide- und Moorlandes dem Walde abgerungene Kultur- oder Halbkulturformationen.

Das Schicksal der übriggebliebenen Wälder war aber ein ganz verschiedenes: in England wurden sie relativ wenig verändert, bei uns sehr stark. Tansley, Moss and Rankin ("The Woodlands of England," New Phytologist, Vol. IX, Nr. 3-4, 1910) sind wohl mit Recht der Ansicht, dass die grosse Mehrzahl der englischen Wälder als "halbnatürliche" betrachtet werden kann, als Abkömmlinge der primitiven Wälder, durch Behandlung und Pflanzung nur wenig geändert. Das beruht auf dem Konservatismus der englischen Landeigentümer, auf den Eigentumsverhältnissen (Privateigentum herrscht weit vor), auf dem Vorherrschen des *jagdlichen* Interesses (die Wälder dienen vielfach als Fasanen- und Fuchsgehege, der Holzertrag tritt zurück) und auf der allgemein zugegebenen Rückständigkeit der englischen Forstwirtschaft. So resultiert der für die Phytographen sehr erfreuliche Zustand, dass die allerdings spärlichen heutigen Waldreste Grossbritanniens—wie wir uns ständig überzeugen konnten—die ursprünglichen Beziehungen zu Boden und Klima noch deutlich zeigen.

Dieses Verhalten erklärt auch die starke Betonung des Bodens als Grundlage der Formations-Charakteristik in der Auffassung unserer englischen Kollegen. Sie finden im Gebiet des Gehölzklimas fast überall eine retrogressive Sukzession von Wald durch Gebüsch zum Grasland: ob auf natürlichem oder anthropogenem Wege, ist freilich vielfach strittig. Die noch vorhandenen Waldreste zeigen sich sehr verschieden auf verschiedenen Böden : so ergibt sich ganz natürlich die Tendenz, die Vegetation jeder Bodenart als ein einheitliches Ganzes zu betrachten. Diess umso mehr, als die

[1] Zu vergleichen mit den englischen "Downs," welche gewiss vom prähistorischen Menschen besiedelt waren. [Ed., New Phyt.]

verschiedenen Bodenarten auch gleichzeitig physiographische Einheiten bilden: Lehm, Ton und Sand in den Niederungen, kieselreicher Boden mehr auf Hügeln (Crampton). Bemerkenswerterweise lässt sich auch ein solcher Parallelismus zwischen der geologischen Unterlage und den Schafrassen erkennen (O'Connell, Agricultural Geography). Diese durch Boden und Sukzession zusammengehaltenen Assoziationen nennen die englischen Phytogeographen eine "Formation." Ueber die Berechtigung dieser *Bezeichnung* kann man verschiedener Ansicht sein—dass aber die durch sie zusammengefassten Vegetationen zusammengehören, ist ausser Zweifel. Dabei muss gegenüber einer auf offenbarem Missverständnis beruhenden Kritik betont werden, dass die in den "Types of British Vegetation" unterschiedenen Formationen "auf Lehm und Ton," "auf kieselreichen Böden," "auf Sandstein" *nur für das untersuchte Gebiet gelten;* es wird keinem englischen Pflanzengeographen einfallen, einen tropischen Urwald auf kieselreichem Boden mit den englischen Eichenwäldern in *einer* "Formation" zusammenzufassen!

Ganz anders war die Waldgeschichte im schweizerischen Mittellande: hier haben die wechselnden wirtschaftlichen Bedürfnisse, in neuerer Zeit unter der Führung einer intensiven Forstkultur die Zusammensetzung des Waldes stark verändert und die ursprünglichen Beziehungen verwischt.[1]

Im Mittelalter wurde der Wald ebenso sehr als Weide wie als Holzlieferant benutzt; das führte zu einer Bevorzugung der Eiche, die ja auch Eicheln zur Schweinemast liefert. Unter dem Einflusse des grösseren Holzbedarfes und einer geregelten Forstwirtschaft, welche die Weide aus dem Wald verbannt, wird später die Eiche zurückgedrängt, die Buche begünstigt und schliesslich die Fichte, welche im schweizerischen Mittellande ursprünglich nur spärlich vorhanden war, durch ausgedehnte Reinanpflanzung an Stelle des Laubwaldes gesetzt. In neuester Zeit kommt die Fortswirtschaft von der Reinpflanzung der Nadelhölzer ab und wendet sich wieder mehr den natürlichen Mischwäldern zu. Es ist aber klar, dass durch die starken früheren Eingriffe das ursprüngliche Waldbild ganz verändert wurde.

So zeigt sich die Geschichte der englischen Wälder grundverschieden von der der unsrigen. Aber auch im Verhalten des *Graslandes* finden sich bedeutende besonders wirtschaftliche Differenzen. Wohl sind die Schweiz und Grossbritannien diejenigen

[1] vgl. H. u. M. Brockmann-Jerosch, "Die natürlichen Wälder der Schweiz." Berichte d. schweiz. bot. Ges. XIX, 1910.

Länder Europas, die den grössten Prozentsatz des bebauten Landes der Produktion von Viehfutter widmen: in der Schweiz sind es 40% der Gesamtfläche, 77% des produktiven Areales, in Grossbritannien schwankt der Anteil des Graslandes an der Totalfläche von 50·4 (England) bis 76·1% (Wales), an der produktiven Fläche von 56% (England), bis 78% (Wales). Beide Länder sind von der Natur prädestinierte Grasländer[1] und in beiden spielt die Viehzucht eine Hauptrolle.

Aber die Natur des Graslandes ist grundverschieden: in der Schweiz herrscht im Hügelland und bis hinauf zur Koniferenstufe intensive Mähewirtschaft vor, welche durch starke Düngung oder Ansaat vom ursprünglichen Rasenbestand total verschiedene Assoziationen schafft; die extensiv betriebenen Weiden mit ihrem zwar auch stark trivialisierten, aber doch etwas mehr dem ursprünglichen Zustand sich nähernden Rasen sind im Wesentlichen auf die subalpine und alpine Stufe beschränkt, wie es für ein Gebirgsland die natürliche Folge der klimatischen und Verkehrsverhältnisse ist: die Höhen liefern das Sommerfutter, die tiefern Gelände das bei der durch den Winter gebotenen Stallfütterung notwendige Winterfutter.

In Grossbritannien ein ganz anderes Bild: neben bedeutendem aber seit 1868 steigend reduziertem Getreidebau (siehe oben!) herrscht auch in der Ebene die extensive Weidewirtschaft, (welche am wenigsten Arbeits- und Kapitalaufwand fordert), meistens auf reinem Grasland, in grossen Parken und auf länderweiten artenarmen Heide- und Moorstrecken betrieben, bedingt durch die niedrigen Preise für landwirtschaftliche Produkte und begünstigt durch das Pachtsystem[2] auf Latifundien (87% des landwirtschaftliche benützten Bodens in England bestehen aus Pachtungen!), ferner durch den milden Winter, der es erlaubt, Grossvieh und Schafe fast das *ganze* Jahr hindurch weiden zu lassen. Deshalb ist auch die Heuwirtschaft in Grossbritannien relativ schwach entwickelt: es wird oft nur *ein*

[1] Und in beiden hat seit Mitte des letzten Jahrhunderts die Graswirtschaft gewaltig zugenommen: in ganz Grossbritannien (siehe Brinkmann, Die Grundlagen der englischen Landwirtschaft, Hannover, 1909) sank der Anteil des Ackerlandes an der produktiven Fläche von 1868 bis 1906 von 51·4% auf 41·5% und stieg umgekehrt die Weidefläche von 48·6% auf 58·5%; dieser Prozess war wie in der Schweiz eine Folge der Getreidekonkurrenz des Auslandes.

Also in England. The great fall in prices resulting from the extensive importation of foreign wheat as a result of the removal of import duty has now been checked, the price of English wheat has risen, and a good deal of permanent pasture is again coming under the plough. [Ed., NEW PHYTOLOGIST.]

[2] Doubtful if the leasehold system has this effect [Ed.]

Schnitt genommen, die weitere Nutzung geschieht dann als Weide in den meisten Fällen erfolgt der Schnitt "unter dem Vieh weg" (Brinkmann). Ueppige Fettwiesen wie sie besonders in der Region der Tauchewirtschaft bei uns vorkommen, sahen wir in England nirgends. Dagegen ist der Feldfutterbau stark entwickelt.

Ein floraverändernder Faktor dagegen, der bei uns völlig fehlt, und der wenigstens lokal in Grossbritannien stark wirkt, sind die *Kaninchen*, welche den Rasen stellenweise förmlich scheeren und nur dornige oder sonst geschützte Arten stehen lassen, u.a. *Carduus crispus* und *Senecio Jacobæa*, die dann im Herbst grosse Bestände bilden. Auch auf die natürliche Verjüngung des Waldes haben sie Einfluss, indem sie die Keimpflanzen wegfressen.

Gegenüber diesen die Flora verändernden Faktoren steht ein die natürliche Vegetation erhaltendes Moment, das bei uns gänzlich fehlt: die ausgedehnten für die Jagd reservierten Gelände, für die keine andere Nutzung besteht! Die "Forests" in England die meisten Mittelwälder und ausgedehnte Heide- und Moorflächen im Norden Englands und in Schottland (die als "Grouse-moors," dem schottischen Schneehuhn als Gehege dienen) gehören hieher.

Zu diesen weiten Flächen landwirtschaftlich unbenutzten Bodens kommen noch die ausgedehnten, höchstens als Streu benutzten *Pteridieten*, an Stelle degenerierter Wälder auf kalkarmem Boden im Norden und Westen Englands und in Schottland in enormer Ausdehnung auftretend. Auch die weiten Hänge der " Pennines " mit magerem Grasland auf kalkarmen Boden werden wirtschaftlich fast nicht benutzt.

So sehen wir zu unserem Erstaunen in dem dichtbevölkerten England enorme Strecken extensiv oder gar nicht bewirtschafteten Bodens, in starkem Gegensatz zu der intensiven Bodenbenutzung unseres schweizerischer Mittellandes.

3. Beim Vergleich der subalpinen und *alpinen* Vegetationen der schottischen Hochlande, die wir auf Ben Lawers (1220^m) kennen lernten, mit ihren biologischen Aequivalenten in den Schweizeralpen ergeben sich etwa folgende Hauptdifferenzpunkte:

(*a*). In den unteren Lagen (unterhalb der Baumgrenze, in der Stufe der " Weide und des geschlossenen Moorlandes " von Smith) sind die schottischen Berge weit monotoner, von ausgedehnten artenarmen zusammenhängenden Moor- und Weideflächen bedeckt (bei Ben Lawers vorwiegend Grasland, sonst meist Heide und Moor), während bei uns Wald, Wiese, Weide, Moor, Geröllflächen, und Felsabstürze, viel mannigfaltigere Vegetationsbedingungen bieten.

Das Fehlen der Sennhütten steigert noch die Monotonie der Land-schaft denn eine eigentliche " Alpwirtschaft " gibt es nicht; die Milchwirtschaft tritt gegenüber der Aufzucht zurück.[1]

(*b*). Die Entwaldung ist weiter vorgeschritten als in unsern Bergen: am Hang von Ben Lawers fehlt der Wald völlig mit Ausnahme einiger angepflanzter Gehölze von *Pinus* und *Larix*.

(*c*). Die Baumgrenze liegt in den Grampians bei *c*. 600^m (610-620^m nach Hardy, 640^m am Ben Nevis nach Berghaus). Die Grenzbäume in den schottischen Hochlanden sind *Pinus sylvestris* var. *scotica* E.u.H. und *Betula tomentosa* Reitt.u.Abel, wobei nach W. G. Smith (brieflich) *Pinus* meist die obere Waldgrenze bildet. *Pinus sylvestris* hat ihre obere Grenze in den Schweizer Alpen einerseits bei 1300^m (Nordalpen) anderseits bei *c*. 2300^m (Puschlav, Südalpen nach Brockmann); ersteres ist die durch Schneedruck leidende typische Form, letztere die dem Schneedruck gut wider-stehende alpine Rasse *engadinensis*. Mit welcher der beiden wir die schottischen Vorkommnisse zu vergleichen haben, ist unsicher. Lassen wir also *Pinus* aus dem Spiel! *Betula tomentosa* geht in den

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[1] W. G. Smith schreibt mir darüber freundlichst folgendes : " Man kann mit Sicherheit behaupten, dass Alpwirtschaft desshalb auf unsern Hochlanden unmöglich ist, weil das Grossvieh dort nicht grasen kann, wo das schottische Schneehuhn und das Rotwild gehegt wird. Es gibt nur sehr wenige Gegenden unserer Hochlande, wo nicht das eine oder andere dieser Jagdtiere gehegt wird, denn wo diess möglich ist, bringen sie dem Landeigenthümer grösseren gewinn als Grossvieh oder Schafe. Folgender Ausspruch stammt von einem erfahrenen Grossgrundbesitzer in d. Hochlander, Lord Lovat (" Afforestation in Scotland," Vol. XXV, Transactions Royal Scottish Arboricultural Society, 1911). 'In Glen-More (in der Nähe des Caledonischen Kanals) ergab die Schafweide selbst in der besten Periode der Schafhaltung nicht einmal 1/5 des Ertrags, den dasselbe Land jetzt als Rotwildgehege abwirft.' An einer andern stelle sagt er : c. Mittleres Rotwild-Land wirft per Jahr 1·3 shillings per Acre (0·4 Hectar) ab ; Schneehuhn-Gehege 1-1½ shillings, Schafsömmerung 1-3 pence.' In diesem Werk über die Aufforstung von Gebirgs-ländereien wird das Grossvieh kaum erwähnt, während die Schafweide häufig berührt wird, ein Beweis für die Rich-tigkeit meiner obigen Behauptung.

" Aber ich glaube, dass im 18. Jahrhundert das Grossvieh auf die höher gelegenen Weiden getrieben wurde. Ich habe das in Werken aus jener Zeit gelesen ; und es ist allgemein bekannt, dass vor etwa 150 Jahren die Schafweide in d. Hoch-lander enorm zugenommen hat, und sich seither erhalten hat, obwohl in den letzer 60-70 Jahren die Schneehuhn-Moore und Rotwild-Gehege zugenommen haben. Wir haben auch richt-bare Beweise dafür, dass das Vieh früher dort oben weidete, denn hin u. wieder findet man in d. Bergweiden zerstreut sogenannte " Shielings," kleine roh gemauerte Hirtenhütten, die jetzt zerfallen sind. Und in Lawers village sagte man mir, dass man früher das Grossvieh auf d. höhern Weiden sömmerte. Doch waren das zweifellos nur junges Masteich (stirks) ; Käse u. Butter wurde dort oben nicht fabrizirt."

Nordalpen bis 1600ᵐ (Wartman u. Schlatter), in den Centralalpen (Berninagebict) bis 2050ᵐ (Rübel), im Ofengebiet bis 2120ᵐ (Furrer, briefl. Mittl.).

Es ist schon seit Wahlenberg bekannt, dass das ozeanische Klima die polare Baumgrenze nach Süden verschiebt; neuerdings hat Dr. Brockmann-Jerosch in zwei sehr bemerkenswerten Abhandlungen auch die Depression der *vertikalen* Baumgrenze durch ozeanisches Klima behandelt.[1] Nach allgemeiner Ansicht steht die Baumgrenze in Schottland tief; der Vergleich mit den Alpen und den deutschen Mittelgebirgen spricht dafür.

Verweilen wir einen Augenblick bei dieser Frage !

Ob die Quote von 600ᵐ als eine relativ tiefe zu bezeichnen ist, ist schwer zu entscheiden.   Denn der Vergleich der Baumgrenzen verschiedener Gebirge ist eine komplizierte Frage.   Vergessen wir nicht, dass eine bestimmte Baumgrenze in vergletschert gewesenen Gebieten kein physikalisch-meteorologisches, sondern ein physiologisch-historisches Problem ist: es ist diejenige Grenze, die ein bestimmter, unter den auslesenden Bedingungen der postglacialen Zeit in das betreffende Gebirge eingewanderter Baum unter den gegenwärtigen Bedingungen durch seine ganz bestimmten oekologischen Eigenschaften zu erreichen im Stande ist.   Ein Vergleich zweier Baumgrenzen ist, streng genommen, nur dann gestattet, wenn sie vom gleichen Baum gebildet werden; und selbst dann ist die Möglichkeit nicht ausgeschlossen, dass der Unterschied in der erreichten Höhe auf einer differenten oekologischen Anpassung beruht (dass zwei geographische "Rassen" vorliegen, wie bei *Pinus sylvestris*).   Dann muss entschieden werden, ob die jetzige Baumgrenze eine natürliche ist oder nicht; und wenn eine ehemalige höhere Grenze, wie das in den schottischen Hochlanden und in den "Pennines" der Fall ist, aus Baumrelikten im Torf konstatiert werden kann.[2]   So taucht die Frage auf: ist diese ehemalige höhere Grenze durch klimatischen Faktoren bedingt (wie Lewis und Crampton annehmen) oder ist die jetzige Depression eine anthro-

[1] Siehe Brockmann-Jerosch " Der Einfluss des Klimacharacters auf die Pflanzengrenzen." Bericht über die 10. Zusammenkunft der freien Vereinigung der Systematiker und Pflanzengeographen in Freiburg i/Br., 1912. Engler's botan. Jahrbücher, 1912.

Und Brockmann-Jerosch und Rübel, " Die Einteilung der Pflanzengesellschaften nach oekologisch-physiognomischen Gesichtspunkten," Leipzig, 1912, bei W. Engelmann.

[2] In den Penninen wurde Birke und Erle in 745ᵐ gefunden, in Schottland Birke und Kiefer bis 1000ᵐ (Lewis') ; nach Hardy ist in Schottland eine Depression der Baumgrenze von 150-200ᵐ zu konstatieren.

pogene Erscheinung (wie die Mehrzahl der englischen Phyto-
geographen glaubt) oder vielleicht lokal durch Facieswechsel
bedingt (Absterben der Bäume durch Aufwachsen des Torfs).

Zum Vergleich des Klimas der schottischen Hochlande mit dem
der Alpen möge hier eine kleine Tabelle über die klimatischen Daten
der Gipfelstation des *Ben Nevis*, des *Pilatus* (mit ähnlicher mittlerer
Jahrestemperatur) und des *Gäbris* im Kanton Appenzell (von
ähnlicher Höhe) folgen :—

1. Ben Nevis, bei 56°48 NB ; 5°8 WL ; 1342ᵐ ü.M. (20 Jahre-
beobachtet).[1]

2. Pilatus, bei 46°59 NB ; 8°16 EL ; 2068ᵐ ü.M. (schweiz.
nördl. Kalkalpen,[2] 10 Jahre).

3, Gäbris, bei 47°23 NB ; 9°20 EL ; 1250ᵐ ü.M. (schweiz.
Molasse-Voralpen,[3] 20 Jahre).

	BEN NEVIS.	PILATUS.	GÄBRIS.
Mittlere Jahrestemperatur	... −0·3 ...	... +0·3 ...	... +5·1 ...
Januar-Mittel	... −4° ...	... −6·2 ...	... −1·9 ...
Juli-Mittel	... +5° ...	... +8·1 ...	... +13·4 ...
Mittlere Jahresextreme	−13·8 ; +16·5	−25·2 ; +22·6	−15·6 ; +25·2
Mittlere Jahresschwankung Diff.zw.Jan.u.Julimittel	... 9° ...	... 14·3 ...	... 15·3 ...
Jährl. Niederschlag ...	... 4084ᵐᵐ ...	... 1393ᵐᵐ ...	... 1336ᵐᵐ ...
Zahl der Tage mit Niederschlag	... 267·2 ...	... 167·1 ...	... 150·7 ...
Nebelfreie Tage ...	... 114 ...	... 225·6 ...	... 258·7 ...

Das Klima des *c.* 10° nördlicher und *c.* 12° westlicher gelegenen,
Ben Nevis ist also gegenüber dem des ungefähr gleich hohen *Gäbris*-
Gipfels ausgezeichnet durch :—

eine um 5·4° niedrigere mittlere Jahrestemperatur,

ein um 2·1° niedrigeres Januarmittel,

ein um 8·4° niedrigeres Julimittel,

eine weit geringere Jahresschwankung (9° gegen 15·3°),

[1] Siehe: Obermayer, Ad. Zwanzig Jahre meteorolog. Beobach-
tungen auf dem Ben Nevis. Jahresbericht des Sonnblick-
Vereins für d. Jahr 1906, Wien 1907.

[2] Buchan and Omond, the Ben Nevis Observations, 1893—1897.
Transact. of the R. Soc. of Edinburgh, Vol. XLIII, 1905.

[3] Maurer, Billwiller u. Hess, Das Klima d. Schweiz., 1910, Bd. II.

eine weit grössere Niederschlagsmenge,

viel häufigere Nebelbildung.

Fügen wir noch hinzu, dass der Wind häufig und heftig ist
(nur 114 Kalmen und eine mittlere Windstärke von 6·5 Sekunden-
metern wurden beobachtet), dass die wirkliche Sonnenscheindauer
nur 16% der möglichen beträgt, der Schnee gewöhnlich von Mitte
November bis Juni liegt und im April eine mittlere Höhe von 2·13^m
zu erreichen pflegt : so bekommen wir einen Begriff von dem
Nebel,- Regen- Schnee- und Sturmreichen, Sonnenarmen ozea-
nischen Klima der schottischen Hochlande.

Wenn wir die jetzige Baumgrenze der *Betula tomentosa,* die
am Ben Nevis bei *c.* 640^m liegt, auf ihren thermischen Wert hin
mit der Birkengrenze in den Schweizeralpen vergleichen, so
kommen wir zu folgendem Resultat :

Am Ben Nevis macht *Betula tomentosa* gegenwärtig bei einer
mittleren Julitemperatur von 9·75°C Halt,[1] während sie bei uns
in den Nordalpen (1600^m Murgtal, Curfirsten) bei einer Julitem-
peratur von 10° (von Glarus aus berechnet), ihre Grenze erreicht;
in den Zentralalpen liegt die Grenze im Berninagebiet bei 2050^m,
entsprechend einer Julitemperatur von 10°, von Sils Maria aus
berechnet; im Ofengebiet liegt sie bei 2120^m, was einer Julitemperatur
von 9·67° entspricht, von Schuls aus berechnet. Am Ben Nevis
erreicht also heute die *Betula tomentosa* ihre obere Grenze unter nahezu
gleichen Temperaturbedingungen des wärmsten Monats wie in den
Alpen. Richtiger wäre der thermische Vergleich, wenn wir die
Mitteltemperaturen der *Vegetationsperioden* vergleichen können,
aber wir kennen die Dauer derselben für die Birke an ihrer oberen
Grenze nicht, und müssen desshalb als ungefähren Masstab
derselben den wärmsten Monat nehmen.

Die Birke macht also am Ben Nevis bei ungefähr denselben
Mitteltemperaturen des wärmsten Monats Halt, wie in den Alpen ;
die so verschiedene Quote ihrer oberen Grenze (640^m Ben Nevis,
1600^m Nordalpen, 2050^m bis 2120^m zentrale Massenerhebung der
Alpen) liegen bei annähernd derselben Mitteltemperatur des Juli
(unter Berücksichtigung der ehemaligen höhern Grenze in den
schottischen Hochlanden sogar bei einer tiefern Julitemperatur, was
einer Hebung der Grenze gleichkäme, wenn das Klima gleich
geblieben ist).

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[1] Julitemp. in Fort William 13·9°C, in Ben Nevis 5°C, Höhen-
differenz 1333^m, macht 0·66° Abnahme der Julitemperatur
pro 100^m ; in den Alpen rechnet man im Mittel 0·65° pro 100^m.

Während aber in den Grampians diese Birkengrenze gleich-
zeitig der Baumgrenze entspricht, liegt im Berninagebiet die
mittlere Baumgrenze (Lärche und Arve bis 2300^m) noch 250^m weiter
oben, also bei einer mittleren Julitemperatur von nur 8°; im ther-
mischen Vergleich mit den Zentralalpen ist also die Baumgrenze
am Ben Nevis um 250^m niedriger, um 300^m im Vergleich mit den
Nordalpen. Es wäre zu untersuchen, ob nicht mit Hilfe der Lärche,
die in Schottland trotz ihrer sonstigen continentalen Allüren vortreff-
lich gedeiht, die Baumgrenze in den schottischen Hochlanden höher
getrieben werden könnte.

Die obigen Ausführungen beweisen die Komplikation des
Problems und rufen einer Untersuchung darüber, ob nicht die die
Baumgrenze deprimirende Wirkung des ozeanischen Klimas vor-
wiegend oder ausschliesslich auf der Herabsetzung der Temperatur
der Vegetationsperiode beruht, und ferner darüber, in wie weit
historische und Concurrenz - Factoren durch Einwanderungs
hinderung hochsteigender Bäume die Grenzfrage beeinflussen.
Doch kann hier darauf nicht weiter eingegangen werden.

(c.) Die alpinen Formationen sind weit weniger mannigfaltig
als in den Alpen ; als geschlossene Formation wird nur " alpines
Grasland " zitiert, als offene die Felsflora ("arctic-alpine chomo-
phyte Formation of crags and corries ") und die Flora des tief-
gründigen und durchlässigen Bodens auf verwitterten windgefegten
Gipfelplateaus (eine vorwiegend *klimatische* Formation).

Es fehlen unsere alpinen Strauchgürtel ; es fehlen Æquivalente
für unsere Alpenrosen, Alpenerlen und Legföhren ; es fehlen die
üppigen Hochstaudenfluren geschützter humusreicher Stellen; es
fehlen analoge Bestände wie diejenigen von *Carex curvula* und *firma*.
Dagegen fanden wir auf dem Gipfelplateau des Ben Lawers in
typischer Ausbildung die "Schneetälchenvegetation," die seither von
W. G. Smith,[1] von dort in ausgezeichneter Weise beschrieben worden
ist. Von ihren konstanten schweizerischen Konstituenten fehlt
Arenaria biflora, Cardamine alpina, Chrysanthemum alpinum und
Alchemilla pentaphyllea, die ersten zwei arktisch, die letztern mittel-
europäisch-alpin.

Dem alpinen Grasland, zu dem auch noch heideartige Vege-
tationen mit *Vaccinium myrtillus* and *uliginosum* gerechnet
werden, fehlt der schöne Schmuck unserer sämtlichen Gentianen
aus der Gruppe Coelanthe (*lutea, purpurea, pannonica, punctata,*
Kochii, Clusii, angustifolia, alpina), ferner *bavarica, imbricata,*

[1] W. G. Smith, Scottish Botanical Review I, 1912.

brachyphylla, auch die alpinen Anemonen, *Pedicularis, Primula* (excl. *farinosa*), *Androsace* vermissen wir.

Subalpines und alpines Grasland und die Vegetation der Gipfelplateaus werden bei näherem Studium noch manche typische Assoziationen aufweisen, ausser den bis jetzt einzig hervorgehobenen Racomitrium-Heiden und Schneetälchen.

4. Die Flora Grossbritanniens ist im grossen Ganzen als eine verarmte mittel- und westeuropäische Flora zu bezeichnen, mit schwachem Einschlag südeuropäischer und amerikanischer Elemente und mit relativ starkem arktischem Einfluss, ohne ausgesprochenen insularen Charakter und mit schwachem Endemismus, der nur durch leichte Flexion der Formen angedeutet ist. Bei der vorgeschrittenen geologischen Reife ("mature physiography" nach Crampton) des Landes überwiegen stabile, ausgeglichene geschlossene, artenarme Pflanzenformationen auf weiten Strecken: Moor, Grasland, und Heide, welche grösstenteils als sekundäre Halbkulturformationen dem in ausgedehntestem Maasse zerstörten Wald gefolgt sind. Durch den Einfluss des Beweidens, lokal auch der Kaninchen, sind diese Bestände trivialisiert und die Unduldsamkeit der herrschenden Arten verhindert erfolgreiche Invasion neuer Formen. *Juncus squarrosus, Nardus stricta, Eriophorum vaginatum, Trichophorum cæspitosum, Calluna vulgaris, Pteridium aquilinum,* herrschen in reinem Schluss auf länderweiten Strecken ebenen oder welligen Bodens. Dazu kommen noch historische verarmende Momente : die relativ geringe Ausdehnung des eisfreien Refugiums im Süden und Südosten England's während der letzten Glaciation und die Schwierigkeiten der postglacialen Einwanderung über Meer.

Aber trotz dieser Artenarmut bot uns Kontinentalen und besonders den binnenländischen Alpenbewohnern unter ihnen die Vegetation Grossbritanniens eine Fülle des Interessanten und Schönen : Die herrlichen Verlandungsbilder und die wilden Bruchwälder ("Carr") in den Broads, die so klaren Sukzessionen auf den marinen Schotterbänken und Salzsümpfen, die Waldbilder und Graslandtypen in den Tälern der Penninen, die stundenweiten ungeheuren Eriophorum-Moore, die oekologisch so verschiedenen Typen der Pteridieten, die Besiedelung und Fixierung der Wanderdünen in Southport, den wunderbaren Baumwuchs von Dunkeld mit seinen säkulären Lärchen, die reiche Wasserflora der "Lochs," die Eichen-Birken-Wälder der "Trossachs" mit ihren üppigen Hymenophyllum-Teppichen, die beinahe subtropischen Wälder

Killarneys mit ihrem *Arbutus*, die Heiden und Bergmoore West-Irlands mit ihren amerikanischen Elementen, die typische Glacial-landschaft, die wir von Urrisbeg bei Clifden überblickten, mit ihrer alle Berge überziehenden Vermoorung und ihren leuchtenden *Ulex-Gallii*-Heiden, die Algenzonen auf den Strandblöcken bei Galway, die cornwallische Heide im jauchzenden Blüten-schmuck ihrer *Erica vagans*, die einzig dastehenden Taxus-Wälder der " Downs " und endlich die mannigfaltigen Wunder, welche ein extrem ozeanisches feuchtes Klima zu Stande bringt : die Verwischung der Höhenunterschiede, so dass *Dryas* und *Adiantum Capillus Veneris* beieinander wachsen, und die reichen Verwilderungsgelegenheiten und unbegrenzten Kulturmöglichkeiten empfindlicher Exoten, wie wir sie namentlich in den Gärten der Herren Beamish und Williams bewunderten.

In der Tat, internationale phytogeographische Exkursionen müssen nach diesem vollen Erfolg des zweiten derartigen Unter-nehmens ein ständiges Bildungs- und Verständigungsmittel der Pflanzengeographen werden: auf Wiedersehen also an der dritten Exkursion[1] in Nordamerika!

[1] Professor Schröter calls the British Phytogeographical Excursion the *second* international excursion, since he claims, with some justification, the Swiss excursion (in connexion with the International Geographical Congress at Geneva in 1908) which he led so ably, and which inspired the initiation of the British Excursion (see New Phyt., X, p. 272), as the *first* inter-national excursion of its kind. [Ed., New Phytologist.]

FLORAL EVOLUTION : WITH PARTICULAR REFERENCE
TO THE SYMPETALOUS DICOTYLEDONS.

By H. F. Wernham.

VIII.   Inferæ: Part II. Campanulatæ.

THE group with which we are about to deal includes those floral forms which are generally regarded as the most highly organized in existence, namely the Compositæ. Their success under the judgment of Natural Selection is evidenced by the enormous number of species (over 11,000) which find a place in this very natural family; and this success reflects the complete realization of all general evolutionary tendencies in combination.

For the rest, Campanulatæ consists of the rather heterogeneous Campanulaceæ, with about 1,000 species ; of Cucurbitaceæ, with somewhat doubtful affinity ; and of three other families with relatively few and highly specialized species.

The large majority of the Campanulatæ are herbaceous ; arboreal or shrubby forms are rare among Campanulaceæ, and rarer still among Compositæ ; and this is in keeping with the great degree of general advance which these groups have attained. There is no extensive arboreal group which stands to Campanulatæ in the same relation, say, as Verbenaceæ to Diovulatæ.

The fundamental tendency of the Campanulatæ is the approximation, and ultimate syngenesis, of the anthers; and this tendency is in obvious relation to pollination. The mechanism in question, often referred to as the " pollen-presentation " mechanism, is familiar to most elementary students. The linear anthers dehisce introrsely, and so discharge their pollen into the interior of the tube formed by their partial or complete union. The young style (the flower being protandrous) is clavate, the stigmas being united until the exserted style is fully grown, and, in the course of its growth it forces its way through the anther-tube, sweeping the pollen gradually before it out of the mouth of the tube ; in typical cases the style is provided with a brush of hairs to facilitate this sweeping process. When the elongation of the style is completed, it projects beyond the rest of the flower; and after a time the stigmas mature and separate, and present their receptive (ventral) surfaces to insect-visitors, inviting them to leave pollen collected from other flowers in the manner

already described. In some cases (many Compositæ) the stigmatic surfaces ultimately curl completely over and so come in contact with any pollen that may remain on the then almost withered andrœcium ; in this way self-pollination is ensured in the event of failure in cross-pollination,—although every chance of success is provided first for the latter process.

The mechanism is both simple and effective, and the " pollen-presentation tendency " is reflected in the largest known natural group of flowering plants. Special modifications of the simple mechanism we have described are expressed in families like Goodeniaceæ and Candolleaceæ; but their distribution is strictly localised and their species are few.

Such is the determinant tendency of Engler's Campanulatæ as a whole, Cucurbitaceæ excepted ; and this, we shall urge, affords the justification for regarding them as the descendants of a common stock as recent in descent as that of the Rubiales, but distinct therefrom. To this matter we shall return shortly,

Second to the pollen-presentation tendency is one which we have met in the Rubiales and their ancestors, the tendency to aggregation of florets ; but in Campanulatæ it plays a much more extensive part. The method by which the aggregation is tttained is, moreover, not the same in the two cohorts ; thus the heads of Dipsacaceæ are the outcome of cymose branching, while those of Compositæ are essentially racemose. The importance of this distinction is seen in relation to the less advanced types of inflorescence in the respective groups ; in other words, the distinction expresses itself in the difference between the two stocks, campanal and rubialian. In the latter the inflorescence-unit is conceived as being characteristically a cymose umbel ; in the former the flowers would be arranged typically in a simple raceme, as occurs in many Campanulaceæ. The essence of cymose branching is the discouragement, so to express it, of single vertically elongated axes, and so the flowers readily tend to be brought to one horizontal level ; in the racemose branching the reverse is the case. As a result we are furnished with a fundamental criterion between the campanal and rubialian stocks, and so the critical character of syngenesis of anthers in the former receives a measure of substantiation. In any case the umbellate type of inflorescence familiar, *e.g.*, in Cornel, Ivy, Elder, Valerian, etc.,—all belonging to families relatively near to their respective stocks (see fig., p. 230)— rarely occurs in the family which includes Harebell and Lobelia.

For the rest, the tendency to oligomery of the andrœcium which marks the progeny of Rubiales is absent in Campanulatæ; and even when zygomorphy occurs of that type which concerns each individual flower, as in *Lobelia* and its allies, this is unaccompanied by any reduction in the number of stamens. This is conceivably in relation to the formation of an anther-tube for the purposes of pollen-presentation ; the sole exception is afforded by the very specialized Candolleaceæ, in which the stamens number two only and are fused with the style to form an irritable *gynostemium* (*infra*), comparable in complexity only with Asclepiads or Orchids.

Campanulaceæ. The essential floral characters of Campanulatæ are shewn in the table in the preceding chapter, p. 219. Setting aside Cucurbitaceæ for the moment, Campanulaceæ, the family second only to Compositæ in number of species, display the widest range of variation. This fact, coupled with the arboreal or suffruticose nature of not a few species, leads to the supposition that Campanulaceæ represent the nearest approximation to the stock to which the Campanulatæ owe their origin—the Campanal Stock.

In Campanulaceæ the anthers of the isomerous andrœcium exhibit every degree of syngenesis, from complete mutual freedom to close union (*Lobelioideæ*) ; in the former case the process of pollen-presentation may take place in the bud. The corolla ranges in symmetry from actinomorphy to the strong zygomorphy seen in the split corollas of Lobelioideæ. The inflorescence is typically a raceme, conspicuousness being obtained by enlargement of the individual flower; but the tendency to aggregation is observable and the capitulate inflorescence is attained, *e.g.*, in *Jasione*, *Phyteuma*. The ovary is usually polycarpellary, multilocular, and multiovulate; but there is a distinct tendency to a bicarpellary ovary, unilocular by reason of the imperfection of the septa.

An interesting feature of Campanulaceæ is the relative position of the ovary, which is not infrequently semi-superior ; or, at least, not entirely inferior. The tendency to epigyny is thus not completely worked out in the Campanal Stock ; and this is suggestive of its *direct* derivation from the rosalian plexus, in contrast with Rubiales, derived as we have seen from an archichlamydeous branch-ftock in which the tendency to epigyny is already fully realized—the Umbellifloral Stock. In the Rosales, as we have already seen, the tendency to epigyny is actively at work, and we take the measure

of this activity by the extreme variability of the relative position of the ovary within undoubtedly close circles of affinity, even within the same genus (*Saxifraga*). The character in question offers an excellent example of the differing critical value of a single character in different groups and for different purposes: in Rosaceæ epigyny may serve only to distinguish one species from another ; in the higher Sympetalæ it may be of cohortal value. In any case the value of any given character can only be judged in relation to the history in descent of the groups to which it is to be applied as a criterion.

Origin and Affinities of Campanulatæ. From the plexus of polypetalous groups in which the tendency to epigyny is clearly traceable we have recognised already the emergence of one line,— that leading to Umbelliflorae, and so indirectly to Rubiales. We are now dealing with a distinct line, leading to the Campanal Stock, determined by sympetaly and by the pollen-presentation tendency; the line is distinct from the rubialian fundamentally, namely, in the last-named tendency, and in the character of the inflorescence.

The Campanal Stock will thus be defined as including hemi-epigynous and epigynous forms, with anthers in various stages of approximation ; the ovary, like that typical of Rosales, will be multilocular and multiovulate. In the Rosales the andrœcium is usually in two whorls, but there are no representatives of this con-dition among their sympetalous derivatives [1]; we are, in fact, confronted with the same lack of transitional (heteromerous) forms in this regard as in the case of Contortæ (chapter IV). The existing group which approximates most nearly to the Campanal Stock as we have defined it, is the tribe Campanuloideæ of Campanulaceæ, which includes mostly forms with regular corollas. But the tendency to zygomorphy in the individual flower is trace-able in a closely continuous series of forms among Campanuloideæ‘ Cyphioideæ and Lobelioideæ ; and this tendency is one of the two which determine two evolutionary lines leading from the Campanal Stock (see diagram in the preceding chapter, p. 230). The line in question terminates with Goodeniaceæ, characterized by the presence of a special cup or indusium formed about the stigma for the purpose of collecting the pollen and so facilitating its presenta-tion ; " this indusium is foreshadowed in the definite rings of hairs occurring below the stigma in some Campanulaceæ. As a diver-gent offshoot from this line stand the *Candolleaceæ*, in which the

[1]   See, however, the remarks on Vaccinioideæ, *infra* p. 300.

complexities in relation to pollination involve the reduction of the androecium to two stamens, which are fused together and with the style to form a gynostemium. The stigma lies in a cavity at the apex of this columnar structure, and is concealed by the anthers ; at a touch from a visiting insect the irritable column springs from one side of the flower to the other, dusting the visitor with pollen, and at the same time exposing the stigma. The mechanism provides a very specialized form of pollen-presentation.

Goodeniaceæ are of especial interest in so far as they exhibit features which connect them with the ancestral Campanal Stock on the one hand and with Compositæ on the other. In the first place, epigyny is not an established character ; the ovary is not uncommonly semi-superior. The tendency to reduction in carpels, loculi, and ovules, is clearly traceable ; normally the ovary is bilocular with few ovules in each loculus. In some cases the septum is imperfect ; in others there is but a single ovule in each loculus. The climax of these tendencies is reached in Brunoniaceæ,—now generally regarded as a tribe of Goodeniaceæ. Its affinities with the latter are obvious, in view of the indusiate stigma of the *individually* zygomorphic flowers ; but the group would appear to have some claim to family rank, with the critical characters of the inflorescence, which is an involucrate capitulum, and of the ovary, which is unilocular, with a single ovule, and quite superior. The case would appear to be one of evolutionary advance con-vergently in the direction of Compositæ, and this is indicated in the diagram on page 230 ; the pappose calyx of the latter is fore-shadowed in the setaceous feathery calyx-segments of *Brunonia*. But the essential affinities of the latter with the line of Goodenia-ceæ are recognizable in the light of the individual zygomorphy of the flowers, and the superior ovary.

Compositæ. The other line leading from the Campanal Stock is determined by the aggregation of flowers, which culminates in the composite capitula. This aggregation is accompanied—conceivably in the relation of cause and effect, by reduction of the ovules to one, contained in an inferior unilocular ovary composed of two carpels. The bicarpellary condition as the climax of the economy tendency in the ovary has been insisted upon and illustrated from time to time throughout these chapters ; and the solitary ovule borne in the unilocular ovary is obviously in keeping with the close approximation of the florets, if only in respect of the merely phy-sical consideration of space. Again, the biological advantage of

this arrangement is clear. The dense aggregation of the flowers permits of the pollination of several at a single brief visit from an insect—and this operates in the way of compensation for any disadvantage accruing from the presence of one ovule only in each flower. The high degree of certainty of pollination has been indicated earlier in this chapter. Lastly, the advantage of a fruit-body for each individual seed (chapter V) is secured, and the calyx, needed no longer for the purposes of protection is utilized for the important function of dispersing this fruit, in virtue of its modification into a pappus; a similar condition has already been described for the Dipsacales (chapter VII).

The composite head, from the aspect of insect-attraction, is the biological equivalent of a single flower. This condition results primarily from the development of a " ray " series of florets, usually the product of extreme zygomorphy, sometimes the mere increase in relative size, of the exterior members of the inflorescence; the latter are usually unisexual (female) or in some cases quite sterile, as in *Viburnum*, noticed in the preceding chapter. The zygomorphy is typically of that peculiar kind expressed in the so-called *ligulate* floret; and in one extensive section of Compositæ, Ligulifloræ, generally regarded as including the most advanced genera, zygomorphy has invaded the whole capitulum, which consists entirely of ligulate florets.

It is worthy of note that, given the cohesion of the anthers to form a tube, the actual mechanism of the pollen-presentation in Compositæ and Campanulaceæ amounts to nothing more than the growth and development of a part of the flower, the style; and the mere simplicity of this arrangement is doubtless much in its favour from the standpoint of biological advantage, in contrast with the subtleties of specially-developed organs like the " pollen-cup" of Goodeniaceæ and the irritable gynostemium of Candolleaceæ.

Referring again to the evolutionary tree of Campanulatæ, (diagram, p. 230), it will be gathered that the line of aggregation is clearly distinct from the line of zygomorphy in the individual flower; the two lines emanating from the Campanal Stock are thickened in the diagram. A transitional stage along the aggregation line is reflected in a small family, *Calyceraceæ*, characterized by definite involucrate capitula and by the presence of a single ovule only in each floret : but there is no zygomorphy of the outer florets, nor is the calyx materially reduced.

Cucurbitaceæ. There remains for consideration one family included in Engler's Campanulatæ, the Cucurbitaceæ. This is a large group, including over 650 species of characteristic habit and facies, inhabiting tropical regions for the most part. These are chiefly annual herbs of rapid growth, climbing by means of tendrils, with palmately veined and lobed leaves ; and the relative constancy of this habit, together with the prevalent separation of the sexes in the flowers (they are rarely hermaphrodite), suggests that Cucurbitaceæ are a specialized family, standing high and terminally upon their particular shoot of the evolutionary tree.

The calyx and corolla, which are both regular, are respectively gamosepalous and gamopetalous, and the latter character affords the justification for including this family in Sympetalæ, as in Engler's system. In previous systems, notably those of Bentham and Hooker and of Warming, Cucurbitaceæ have been classed with polypetalous groups, in spite of their prevailingly sympetalous corolla, for reasons which we shall endeavour to discuss presently.

The andrœcium is of particular interest, and it affords the basis for the sub-division of the family.[1] The fundamental type of andrœcium consists of five stamens (*i.e.*, isomerous with the corolla), each with a bilocular anther ; this condition characterizes the tribes Fevilleæ, in which the filaments are free or almost free, and Sicyoideæ, in which the filaments are united to form a column. These two tribes comprise, however, only about 20% of the total number of species in the family. In the majority of cases, together representing about 63% of the family, the andrœcium consists of three stamens—two with quadrilocular anthers, and one with a bilocular anther. The structure of the quadrilocular pair in the several forms is strongly suggestive of their origin by fusion in the course of descent[2] ; and this, according to Payer,[3] is borne out by the facts of the floral ontogeny.

Taking the bilocular microsporangium, then, as a unit, the andrœcium in these apparently triandrous flowers typical of Cucur-bitaceæ may be, in a phylogenetic sense, really pentamerous and isomerous with the corolla. The anther-sacs are variously elabo-rated in different forms as the result of elongation and curvature into S- and U- shapes, and the fusion is very diverse in degree, as

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[1] According to Pax, in Engler, *Die Natürlichen Pflanzenfamilien*, IV. 5, p. 10.

[2] See the figures of various types of cucurbitaceous andrœcium in Engler, *loc. cit.*, p. 5.

[3] *Traité d' Organogénie comparée de la Fleur*, p. 441.

affecting both anthers and filaments. The climax is reached in the tropical American genus *Cyclanthera*, with over 30 species, *i.e.* (about 5% of the family), in which the anthers are fused into a ring, divided into two chambers along its length, and seated upon a column composed of the united filaments.

There is, moreover, a tendency to oligomery of the andrœcium ; about 10% of the family is concerned. In *Gerrardanthus* (4 spp.) the andrœcium consists of four stamens and a staminode ; in *Gurania*, *Anguria* (over 70 spp.), etc., only two stamens are present in each flower. This tendency, coupled with the curiously twisted anther-sacs, might be urged to support the affinity of Columelliaceæ (chapter VI, p. 154) with Cucurbitaceaæ ; but in view of the specialized habit and polycarpellary ovary of the latter, and their close relationships with Parietales, it seems improbable that the shrubby, bicarpellary Columelliaceæ have any near connection with them. The affinity of Columelliaceæ with Gesneraceæ is much more apparent (see chapter VI).

The ovary in Cucurbitaceæ is invariably inferior, and is composed usually of a number of carpels exceeding two. The usual number is three, but the gynæcium may be isomerous with the corolla, or it may be reduced to a single carpel. The number of ovules present is variable, from a single one to an indefinite number. The ovary is primarily unilocular,[1] the ovules being borne upon parietal placentæ; but in typical cases the latter project so far into the cavity of the ovary as to meet and form a central column, and the ovules are carried upon the recurved productions of the placentæ beyond this. The ovary thus becomes secondarily septate ; the structure can be studied conveniently in thin slices from a cucumber.[2]

The prevailingly sympetalous corolla, the cohesion in the andrœcium, and the multilocular inferior ovary with indefinite ovule-number suggest, superficially at any rate, affinity with the Campanulatæ—a suggestion actually adopted in Engler's system. We would urge, however, that this resemblance does not lie very deep. The sympetalous corolla alone can afford no guide to affinity. There is, it would seem, a fundamental difference between the staminal cohesions in Cucurbitaceæ and the syngenesis of anthers in Campanulatæ. The latter is referable to a definite biological purpose,

[1] Payer, *loc. cit.*, pp. 442-3, and plate 81, figs. 15-37.

[2] See also Lindley, *The Vegetable Kingdom*, Third Edition, fig. CCXVIII., p. 313, in which the true structure is displayed with remarkable clearnes

pollen-presentation; but no such phenomenon is to be associated with cucurbitaceous flowers. The diclinism of the latter, and, more important still, the regularly *extrorse* dehiscence of their anther-sacs, are of essential significance in this connection; for this type of dehiscence is altogether inconsistent with pollen-presentation. Again, the spuriously septate ovary of Cucurbitaceæ, with placentation that is, strictly speaking, parietal, offers no legitimate comparison with the ovary of Campanulatæ, which is primarily septate, from the aspect of both ontogeny and phylogeny.

Indeed, it would seem that Cucurbitaceæ have no near relations among Sympetalæ; truly the nearest resemblance is displayed by the Campanulatæ—a resemblance which we have just found reason to suspect of being little more than merely superficial. But their affinities with Archichlamydeæ are not far to seek,—namely, in the epigynous groups of Engler's Parietales, the Passiflorales of Bentham and Hooker. Here is to be found a strong tendency to separation of the sexes (Begoniaceæ, Datiscaceæ, some Passifloraceæ), to union of the stamens, and to spurious septation of the ovary by the projection of placentæ. The climbing habit, moreover, is a feature widespread among these groups.

Considered as a sympetalous group, Cucurbitaceæ seem to have more in common with Passiflorales than has any other group of Sympetalæ with any other group of Archichlamydeæ, and it would appear to be to the credit of the older systems that this affinity is recognized therein, in spite of the sharp line which is the custom to draw between the sympetalous and the polypetalous series.

Whether, in effect, they be viewed from the aspect of a mere aggregate of characters irrespective of any guiding principle in the estimate of the value of those characters, or whether some sort of biological criterion be applied, as throughout these chapters, Cucurbitaceæ would appear to offer a striking example of the phyletic continuity which subsists between Archichlamydeæ and Sympetalæ; and this by reason of their similarity in essentials to the Passiflorales. Significant in this connection is the isomery of the stamens with the corolla in the extensive family Passifloraceæ—a condition rare among Archichlamydeæ. Sympetalous forms, moreover, are to be found among Passiflorales, apart from Cucurbitaceæ—*e.g.*, in Loasaceæ and Caricaceæ. The latter family, included by Bentham and Hooker in Passifloreæ, comprises about thirty species, all characterized by a sympetalous, tubular corolla; unlike Cucurbitaceæ, nevertheless, they are retained among Archichlamydeæ in Engler's system.

So long as Sympetalæ and Archichlamydeæ are separated sharply as distinct groups, Cucurbitaceæ are entitled a place among the former. But this place, we conceive, must be relatively isolated, in view of the considerations to which we have referred above; and this family cannot be regarded even as emerging from the line which led to the Campanal Stock, but must rather be considered as the immediate sympetalous derivatives of those groups of Engler's Parietales which exhibit the tendency to epigyny.

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Summary of Inferæ.

It may be well at this point to summarize briefly our study of the Inferæ, illustrating our summary with the aid of the evolutionary tree figured on p. 230 in the preceding chapter.

We have recognized, in the short sketch of the Archichlamydeæ furnished in Chapter II, a definite tendency to epigyny along certain lines of descent, and we have suggested that certain biological advantages are attendant upon this character. In the endeavour to secure these advantages, if we may so express it, the several floral forms and groups have doubtless made not a few experiments in the course of descent; in other words, epigyny may be the outcome of more than one morphological modification. One, the progressive hollowing of the thalamus and ultimate fusion of the latter with the carpels, is clearly recognizable in a series of forms. There are, without doubt, others; and epigyny, like angiospermy and zygomorphy, has very probably been attained in more than one way. But the data provided hitherto by research into floral development are, unhappily, so meagre, that any detailed discussion of the matter, invaluable in more fortunate circumstances, must inevitably be barren and misleading in the present state of our knowledge.

We must be content for our purposes, then, with the observed fact of epigyny, however produced, and with a knowledge of the extent of its occurrence among groups which are to be regarded as natural apart from considerations of the relative position of the ovary in the flower.

Beside its very probable origin in more ways than one, we find the occurrence of epigyny in more than one undoubted circle of affinity. In some groups—*e.g.*, Ranales, Sapindale,—epigyny is so rare that it may represent merely the special tendency expressed in a solitary genus (*Eupomatia*) or strictly within the

limits of a single family (Celastraceæ).[1] In other cases epigyny occurs with sufficient frequency to be regarded as the reflection of a slight general tendency, as is seen among Centrospermæ; in this particular example the tendency has impressed itself to a corresponding extent upon the sympetalous descendants Primulales, as, witness the genera *Maesa*, *Samolus*, etc. We must point out, however, that such isolated cases of epigyny as these last admit of an alternative interpretation, namely that the inferior position of the ovary is here not an ancestral character, but represents a tendency initiated in the progeny rather than derived from the stock; such, we have suggested in a previous chapter, is probably the case with Gesneroideæ.

Each instance must be judged upon its own merits; but in any case the question is largely speculative. Broadly speaking, it would seem that, in cases where the tendency to epigyny is approximately no stronger (*i.e.*, characterizes no more species) in the sympetalous progeny than in the ancestral stock, the character in question may be regarded in the progeny as derived from the ancestor. This is the case of Primulales and Centrospermæ. On the other hand, in cases where epigyny characterizes a considerable number of species of relatively close and restricted affinity in the progeny, while it occurs only very rarely if at all in the ancestral stock, it is to be regarded as a tendency initiated in the progeny, and not derived from the stock. This is the case of Gesneraceæ and Geraniales; and this brings us face to face with the problem of the systematic position of the Vaccinioideæ. For the last-named group may not impossibly stand to Ericaceæ in the same relation that we have represented the epigynous Gesneroideæ as standing to Gesneraceæ. We must, then, digress from our summary at this point, in order to complete our study of the epigynous Sympetalæ by the consideration of this problem.

<center>*   *   *   *</center>

<center>VACCINIOIDEÆ.</center>

The alternative aspect of the question, namely, that the epigyny of Vaccinioideæ is an ancestral character, has already been presented in Chapter III; and in the search for an epigynous ancestry we were led to the conclusion that the group in question has been derived from a stock different from that of the rest of the Ericales,—*i.e.*, the Rosalian Stock. If this conclusion be the true

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[1] Calycanthaceæ, a family of Ranales, marks a step on the way to epigyny—the flowers are perigynous.

one, Vaccinioideæ will readily find a place among Inferæ. Significant in this connection are, first, the prevailingly racemose inflorescences, and the absence of any tendency to the "umbelli-floral" arrangement, (chap. VII). Second, the introrsely dehiscing anthers are approximated to each other and to the style, in definite relation to pollination. These two characters point to affinity with the Campanal Stock, as opposed to the Rubialian, in which the inflorescences are umbellifloral and the anthers separate, if not prevailingly divergent. Lastly, this suggestion is not discouraged if we compare the habit and general facies of the Thibaudieæ section of Vaccinioideæ with that of the shrubby and arborescent members of Campanulaceæ.

This line of reasoning, dependent, we repeat, upon the assumption that the epigyny of Vaccinioideæ is an *ancestral* character, leads us in this way to regard the group as representing the Heteromeræ of the campanal stock. In other words, Vaccinioideæ will represent the transition, from the aspect of economy of the andrœcium, between the diplostemonous Archichlamydeæ and their haplostemonous sympetalous progeny—a link which we have failed to find in the case of the hypogynous Sympetalæ, the Bicarpellatæ (chapter IV). In the case of Rubiales, a similar link with Archichlamydeæ is not of similar weight, as isomery of the andrœcium is already accomplished in Umbelliflorae.

Against all this there is, however, an objection which is regarded by most systematists as paramountly serious, namely, the close resemblance between Vaccinioideæ and other groups of Ericaceæ in respects other than that of the relative position of the ovary; and in modern systems the ericalian affinity is universally recognized.

This side of the case has been emphatically stated recently by a well-known British systematist,[1] substantially in the following terms: " If the Vaccinioideæ are to be removed from " the Ericaceæ, the Arbutoideæ must go with them, on the ground " of the specialized characters of the anthers, fruit, and seed .... " the result would be a most unnatural separation, because the " Arbutoideæ and Vaccinioideæ together have many characters in " common with the rest of the family. Hence," he adds, " this " suggestion would result in chaos ! " The "suggestion" was, nevertheless, adopted by no less a philosopher than Lindley, who says : " It is usual to station these plants (Vacciniaceæ) with Heathworts

" (Ericaceæ) to which they bear much resemblance .... They
" are, however, to all appearance closely allied to Cinchonads
" (Rubiaceæ) .... and also to Escalloniads (tribe of Saxifragaceæ)
" which are chiefly known by being polypetalous .... Upon the
" whole, Cranberries (Vacciniaceæ) may be considered as a Order
" standing on the borders of .... the Cinchonal and Grossal (Rosalian)
Alliances." [1]   In other words, Lindley regards Vaccinioideæ as the
sympetalous " Heteromeræ " of the Calycifloral Plexus.

The Vaccinioideæ, then, apart from their epigyny, are linked
with the typical hypogynous Ericaceæ by the tribe Arbutoideæ.
Taking the family Ericaceæ as it stands in Engler's system the tribe
Vaccinioideæ includes little less than a quarter of the total number
of species, that is to say, a considerable portion.   The ancestral
Geranial Stock exhibits no tendency towards epigyny ; if, therefore,
in view of the links which unite Vaccinioideæ with the hypogynous
Ericaceæ, we are to regard them as derived from the same proxi-
mate ancestral stock, we must then suppose that Vaccinioideæ have
adopted epigyny as a special tendency developed after the evolution
of the Ericales.   The case will then offer an exact analogy with that
of Gesneroideæ ; and the Campanulatæ, like the Bicarpellatæ, must
remain without pentacyclic representatives.

The Phyletic History of Inferæ.

Returning to our evolutionary tree, we see at its base an archi-
chlamydeous plexus characterized by a definite tendency to epigyny.
From this plexus two lines emerge,—one determined by the final
realization of epigyny, coupled with the tendency to bring the
flowers of an inflorescence to one horizontal level ; the other
determined by the adoption of sympetaly before epigyny was com-
pletely realized, coupled with the tendency to approximation of the
anthers for the definite biological purpose of pollen-presentation.
Before the latter tendency appeared, Cucurbitaceæ were produced
by the grafting of sympetaly upon one stock of the Calycifloral
Plexus, the Passiflorales of Bentham and Hooker.

The first, or " umbellifloral " line, leads on the one hand, to the
Umbellifloral Stock, determined by reduction in ovule-number,
and on the other to the Rubialian Stock, determined by sympetaly.
The second line leads to the Campanal Stock.

We desire to insist upon the sharp separation of these two lines,
and such similarity as obtains among their ultimate descendants

[1] *The Vegetable Kingdom*, Third Edition, p. 757,

Campanulatæ.

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must be regarded as due to converging development. The main lines of floral evolution are limited and few in number, and we see them recurring again and again in different circles of affinity; this is admirably illustrated in the subsequent genealogy of the Inferæ.

From both the campanal and the rubialian stocks two main branches arise; each of these branches leads to zygomorphy of one or other of the two types suggested in our opening chapter and frequently illustrated since. Thus, zygomorphy induced in the individual flower, *i.e*, apart from aggregation, produced the Lobelioideæ and Goodeniaceæ from the Campanal Stock, and the Dipsacalian from the Rubialian Stock. Aggregation of florets, with consequent zygomorphy, produced Compositæ from the Ccampanal Stock, and Dipsacaseæ from the Dipsacalian Stock. An evolutionary process similar to the last-named, but on a much smaller scale, produced Brunoniaceæ from Goodeniaceæ. The branchings from the Umbellifloral Stock exhibit only one type of zygomorphy, namely, that which results from aggregation, as illustrated in Umbelliferæ. For the rest, the three groups Campanuloideæ and Calyceraceæ; Rubiaceæ and Caprifoliaceæ; Araliaceæ and Cornaceæ; represent respectively the nearest living approximations to the hypothetical stocks which we have postulated,—the second family of each pair reflecting a step in the evolution of the progeny.

The families which stand highest in the tree, *i.e*., Umbelliferæ, Valerianaceæ, Dipsacaceæ, and Compositæ, display two or three notable points of similarity. In the first place, all are characterised by what we may name the fundamental aggregation of flowers into more or less dense inflorescences. This character is absent in the broad sense from the ultimate members of the hypogynous Sympetalæ, the higher Tubifloræ, in which zygomorphy of the individual flower is the key-note of advance. Some sort of relation between the aggregation and the inferior position of the ovary is not difficult of conception ; for the relegation of the actively-developing female parts of the flowers to a secluded position doubtless mitigates any disadvantages of space which might arise from the close aggregation, at the same time discharging an important protective function. Again, the reduction of the ovules to a single one per loculus, which characterizes all the four familes just named, is of clear advantage in the same connection, especially when viewed from the aspect of seed-dispersal. The pappose calyx of Compositæ and Valerianaceæ is readily conceived as advantageous in operating to release the inferior fruit quickly from a

close inflorescence and from a common receptacle.   Dipsacaceæ
and Valerianceæ, in obedience to the tendencies of their ancestral
stock, are exceptional in exhibiting zygomorphy in the individual
florets ; but it must be remembered that, compared with Compositæ
and Umbelliferæ, these two families are exceedingly small in point
of number of species ; so that we may conclude finally that the most
successful tendencies of descent have been those which produced
a densely-aggregated inflorescence, together with the concomitant
and, as we have endeavoured to explain, consequent characters of
zygomorphy, epigyny, and the solitary megasporangium, maturing
into a seed dispersed typically by the aid of a modified calyx.

<div align="center">*   *   *   *</div>

It is in the classification of the Inferæ that the system of
Engler differs most fundamentally from that of Bentham and
Hooker in respect of the Sympetalæ, and some comment upon this
difference may not be out of place.

The difference concerns the union of the families into groups ·
of higher order ; the families themselves are virtually identical in
both systems.   Bentham and Hooker, in associating Valerianaceæ
and Dipsacaceæ with Compositæ and Calyceraceæ (Asterales), and
in separating the group so formed from Campanulaceæ and their
allies (Campanales), have emphasized the uniovulate character of
the ovary to the exclusion of all other considerations.   But our
examination of the ancestry and affinities of the Inferæ has led us
to associate Compositæ with Campanulaceæ, and to separate them
from Dipsacales ; and we have endeavoured to trace the connection
between the last-named group and Rubiales.   General biological
tendencies have been our guide throughout ; and this would seem
to be the proper course in the discussion of the larger plant-
groups.   Seeing that the most advanced plant-forms are concerned,
it is to be expected that the dominating tendencies should be those
associated with adaptation for insect-visitors rather than merely
with economy of reproductive parts ; and in the light of such
tendencies we have been led to the sharp separation of a Campanal
or pollen-presentation series from a Rubialian or umbellifloral
series.   In both series we have met with aggregation of florets
and with reduction in ovule-number ; hence the similarity between
Compositæ and Dipsacaceæ—a similarity which does not, however,
justify the conclusion that these two families have been derived
from the same proximate ancestral stock,—*i.e.,* that they should
be associated in the same cohort.

It would appear, then, that the English system is tainted in this regard, through the undue stress laid on a single and relatively unimportant character; Engler's system, on the other hand, has escaped this objection, and reflects the genealogy which we have attempted to portray. At the same time we have found reason for supporting the place assigned in the older system to Cucurbitaceæ.

We shall, however, have some general remarks to make upon certain principles of classification in our next, the closing chapter.

[*To be concluded*].

TWO FOSSIL PROTHALLI FROM THE LOWER COAL MEASURES.

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[Plates V and VI and Two Text-Figs.]

THERE are but few fossil prothalli preserved to us from the Palæozoic ages, and even among the few that are known a good state of preservation is decidedly rare. This rarity may be due partly to minute size, which hinders their recognition in the matrix, and partly also to their own unsubstantial nature in the first instance.

The two examples here to be described, belong respectively, to the Pteridospermic seed, *Lagenostoma Lomaxii* (Williamson), and to the megaspore of a species of Lycopod (possibly *Bothrodendron*), which it has not been possible to relate with certainty to any parent plant. There is a close resemblance apparent between the figures given by Mr. D. M. S. Watson of the megaspores in *Bothrodendron mundum*, and the present specimen.[1]

Both specimens are in the hands of Professor F. W. Oliver, F.R.S., to whom I am indebted for their use. Taking them in detail, the *Lagenostoma* prothallus will be dealt with first.

[1] Since the above was written Mr. Watson has certified the reality of this resemblance. The spore is therefore to be regarded as belonging to *Bothrodendron*.

I—LAGENOSTOMA LOMAXII (PLATE V).

The gametophyte generation of Pteridospermic plants is known in a variety of cases. In some, merely distorted remains of pro-thalloid tissues have been found, which afford little clue to their original arrangement.

In *Stephanospermum*,[1] however, where " cytological " preserva-tion is unusually perfect, the prothallus has accordingly been found in a state bordering on entirety, showing clearly remains of the archegonia in their natural position. Many seeds described by Brongniart[2] from the Carboniferous and Permian of France—as also specimens of the seeds of *Cordaites*—contain the endosperm and archegonia in a wonderful condition of preservation. The subject of the present description has not hitherto exhibited any such structures, and any remains of megaspore tissue preserved at all have been vague.

The present specimen is a transverse section of the above seed, circular in outline, and bounded by the dark-brown testa with its two concentric bands ; the palisade on the outside, and the prosenchymatous band on the inside, are fairly conspicuous. In the centre is the gibbous mass of fragile-looking tissue which represents the prothallus, lying rather to one side of the section, and entirely free from contact with any of the peripheral structures. (See Plate V).

In a memoir which was published in 1904, Oliver and Scott[3] described in detail a complex seed which had been discovered, in the first instance, by Williamson, although it was left by him undescribed. In his manuscript catalogue, Williamson named this seed *Lagenostoma Lomaxii*, classing it with his two other species of that genus (*L. ovoides* and *L. physoides*) already published in his eighth memoir.[4]

The seed was referred by Oliver and Scott to *Lyginodendron*, on the basis of many features of anatomical agreement with the vegetative organs known to belong to the plant whose stem bears that name.

Since the publication of their description, a fructification

[1] Oliver. " Trans. Linn. Soc., Bot.", Vol. VI, 2nd Series, Part VIII, 1904.

[2] Brongniart. " Recherches sur les graines fossiles silicifiés." Paris, 1881.

[3] Phil. Trans., Ser. B, Vol. 197, 1904, pp. 193—247.

[4] " Organisation of Fossil Plants of the Coal-Measures," Part VIII, Phil. Trans., 1877.

bearing the name of *Calymmatotheca*, found in the form of impressions, has been identified as the rachis upon which these seeds were produced.[1] Despite the absence, even to the present day, of any specimen showing absolute continuity between this female fructification, and the vegetative stem of *Lyginodendron*, the evidences of resemblance are sufficiently strong to preclude any serious doubt that the attribution of the seed upheld by Oliver and Scott is correct. *Lagenostoma Lomaxii* was the first seed recognized as being borne upon a fern-like plant. Being itself so fully known, and belonging to a plant also very fully investigated, it may be considered the most outstanding type of Pteridospermic seed.

The additional specimen which it is proposed now to describe, emanates from Mr. James Lomax, from whom came also the original specimens of the seed. Found at Dulesgate, it came to light only after the publication of the well-known memoir in which all the other sections were described. Enough interest, however, attaches to it, to render a separate notice desirable, as it displays in excellent preservation a structure hitherto unrecorded.

The section (R. 17b Univ. Coll. Colln.), is transverse, being the second of a series of two, cut through the lower half of a single, full-grown seed. The other, the companion section (R. 17a), cuts through the chalazal cushion and the median vascular bundle belonging to it, passing out below the junction of chalazal cushion and testa. A fine section of a pedicel of *Lagenostoma* is also included in this slide. R. 17b is approximately 1 mm. higher up the seed, that is to say it falls within the lower third, and well below the equatorial line. Neither section is absolutely transverse,— R. 17a being inclined about 20°, and R. 17b about 10° to the horizontal.

The section R. 17a is not specially noteworthy. It strongly resembles R. 8a (Pl. 5, fig. 13, O. and S.), and is only mentioned in this connection as enabling the position of R. 17b to be ascertained.

Oliver and Scott describe as typical a shrunken appearance of the internal organs, the megaspore membrane being found in the centre, much crumpled, and closely surrounded by the "intermediate sack," a shrivelled layer representing the nucellus, and a portion of the hypoderm, the "bundle ring," in which the nine vascular bundles are embedded, this being separated from the testa by a wide space called the "outer sack." Such is the appearance shown in their Pl. 7, fig. 2. In the present specimen,

[1] F. W. Oliver, *Farnsämen.*

however, there has been no collapse of the megaspore, and in consequence, not only is the gametophyte tissue itself preserved, but the nucellus and the vascular bundles retain their true relations to the testa, that is to say they are closely adherent to the hypoderm. The exact number of vascular bundles present is difficult to determine, for the reason that, in spite of the excellent preservation of some of the structures in the seed, the bundles themselves are completely rotted away. Judging by the cavities left, the normal number of bundles, nine, seems to have been present.

The nucellus, as mentioned above, is closely adpressed to the inner surface of the integument, and is very shrivelled. Within this, comes a noticeably thick membrane, which shows a granular, and imperfectly preserved appearance. The existing appearance of this membrane is not altogether that of a structure originally simple and truly membranaceous.

I owe to Professor Oliver the suggestion that on the analogy of the similar structure in *Physostoma*, this supposed megaspore-membrane may really represent the remains of a perished tapetum. This is, of course, only a suggestion, and in the present paper the previous appelation of " megaspore-membrane " is provisionally retained.

The actual prothallus is entirely isolated from this membrane. It is incomplete in circumference, about two-thirds of the original circular outline being preserved. At one point it has been violently separated from the megaspore wall, and a few cell-walls remain adherent to the latter. The component cells are naturally very thin-walled, but they have been preserved without much shrinkage, although the tissue of the prothallus is ruptured in several places, leaving large lacunæ. Of contents, there are numerous traces, the most notable being a faint reticulum which occupies some of the cells, and certain opaque granules apparently suspended by filaments in the interior of many of the peripheral cells, both of which appearances are shown in Plate V (lower figure).

The entire section is shown in Plate V. The dimensions of the principal elements are as follows :

Entire Diameter of Seed - - 3·9 mm.
Average Thickness of Testa - - ·2 mm.
Dimensions of Alveoli   Length ·07—·13 mm.
Breadth (average) ·03 mm.

The arrangement of the alveoli in the tissue exhibits features of interest. Round the periphery of the prothallus is developed a

limiting layer of small cells which are roughly square in shape. To this succeeds, centripetally, a wide band of tissue composed of elements radially elongated, while the central portion is occupied by a mass of rounded cells. Unfortunately, these last do not show very plainly in the figure, because, although they are clearer in the original, a large quantity of granular dirt obscures the arrange. ment. This sort of appearance in transverse section is decidedly reminiscent of the prothalli of recent Gymnosperms.

The method of formation of alveoli in the Gymnospermous prothallus was first described by Hofmeister[1] in *Pinus*. He fell
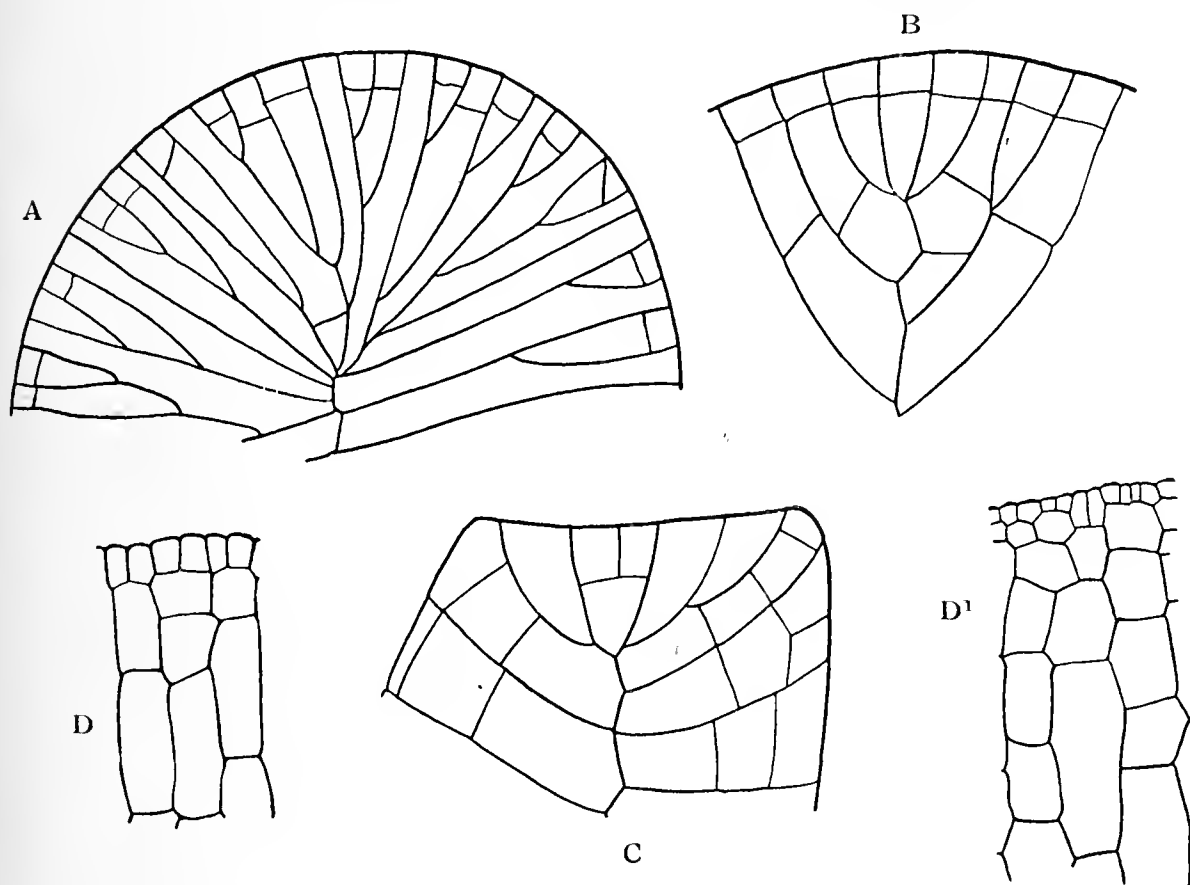
Text-Fig. 1.

A. *Pinus sylvestris.* Part of the longitudinal section of the prothallus. ×106.

B. *Pinus sylvestris.* Upper end of the prothallus, showing the peripheral layer. ×160.

C. *Ephedra vulgaris.* Upper portion of the prothellus. ×160.

D, D[1]. *Dioon edule.* Transverse sections of the prothallus. D is slightly younger than D[1]. ×60.

A, B and C after Mlle. Solokowa.   D, D[1] after Chamberlain.

into the error of supposing that the first endosperm, formed in summer, was a cellular structure developed by ordinary cell-division,

[1] Hofmeister. " Vergleichende Untersuchungen." Pp. 141, 127, 129.

the walls being re-absorbed in the ensuing spring, and the radial structure of the true endosperm produced by a process of centripetal alveolation in the protoplasmic sac.   Strasburger[1] corrected the erroneous view of there being two successive endosperms, but he confirmed the observation of centripetal alveolation, and the resulting radial arrangement of cells.

The whole process has been fully described, in recent years, by Mlle. Solokowa[2] from a number of species of Conifers and Gnetaceæ. The radial type of structure seems, from her work, to be widely distributed among Gymnosperms. In *Pinus* (*sylvestris* and *pumilio*), *Cephalotaxus Fortunei*, and *Ephedra vulgaris*, she figures appearances which seem definitely comparable with what occurs in *Lagenostoma*. There is also a radial arrangement in *Cunninghamia*, although the component cells are not elongated.   Among the Angiosperms, the occurrence of a related type of structure has been recorded by Hegelmaier[3] in *Adonis*.

The text-figures above illustrate some of the arrangements figured by Mlle. Solokowa ; also the arrangement in *Dioon edule*, after two figures given by Chamberlain.[4] Most of the stages shown are fairly young. The radial arrangement tends to become obscured in the tissue of less elongated cells which appears secondarily ; but this is not so in *Araucaria*, where it remains perceptible even during the development of the embryo, and the same is true of *Dioon*. In all cases the differentiation of a peripheral limiting layer of small cells is evident.

The development of a central plexus in the prothallus is noticeable both in *Araucaria* and *Lagenostoma*. In longitudinal sections of the ovule of the recent plant, this plexus is seen to be composed of elongated cells forming a broad bundle which presumably serves as a means of conduction through the middle of the prothallus.   Whether the large development of this tissue in *Lagenostoma* was associated with numerous archegonia, it is impossible to say, the section being cut considerably too low to show any trace of those organs.

The   comparison   with   *Araucaria*,   in   spite   of   the   distance

[1] Strasburger.   "Die Angiospermen u. die Gymnospermen." p. 115.

[2] Solokowa.   Bull. de la Soc. Imp. Nat. de Moscou. Nouv. Sér., Tom. IV, 1890.

[3] Hegelmaier.   Nova acta d. Kais. Leop. Car. Acad. der Naturf, 1885, p. 91.

[4] Chamberlain.   Bot. Gaz., Vol. 42, 1906.

separating the two genera, thus affords some interesting analagies. The transverse section of the ovule of *Araucaria imbricata*, shows, though in a less marked degree, the same characteristics as the fossil.

In Cycads also a similar state of affairs prevails, the relative sizes of prothallus and seed being more comparable with those of *Lagenostoma* than is the case with the Conifers.

It is not necessary to say anything about the testa, as that has been already exhaustively dealt with by Oliver and Scott. In this instance, it is perfectly normal. Disorganised remains of cupule, recognisable chiefly by the rotted out remains of the marginal glands, surround the section, but display nothing of special interest.

Enough has been said, perhaps, to render it a fair conclusion, that *Lagenostoma Lomaxii* possessed a prothallus the arrangement of whose elements resembles that found in the prothalli of recent Gymnosperms, strongly suggesting that it originated in a similar manner, by centripetal alveolation.

The megasporal tissue of *Lepidocarpon*, commonly well preserved, which has an interest in this connection, shows the same marginal layer of small cells, and a similar central plexus, but all appearance of the most significant feature, the radial arrangement in the tissue, is absent.

Oliver, in describing *Stephanospermum*,[1] maintains that *Lepidocarpon* has left no seed-bearing progeny, but that present-day Gymnosperms have originated from an ancestral type characterised by the possession of a pollen chamber. It is not too much to say, that this fresh fragment of evidence, in the Gymnospermous affinities of the prothallus of *Lagenostoma*, tends rather to strengthen the above view.

II—Lycopod Prothallus (Plate VI).

This section was discovered by Professor Oliver among a number of waste slides belonging to Mr. Lomax, and its locality is therefore uncertain, although it is safe to say that it came from the Lower Coal Measures, most probably from Dulesgate. It is preserved in the common state of coal-ball petrifications, that is to say, by mineralization with calcite, and the general state of preservation in the surrounding mass seems to have been of a high quality, judging

[1] Loc. cit., in summary.

from the portions of other plant-tissues occurring in the same preparation.

In general outline this specimen shows a median section of oval form across a thick-walled megaspore which has dehisced, the gap opened by the dehiscence being filled by a large pad or cushion of parenchymatous tissue, which also projects considerably toward the exterior. This pad is considered to represent the prothallus belonging to the megaspore.

In the lower right-hand corner of the prothallus appear vesicles larger than the others. These are the supposed archegonia.

The section passes vertically through the spore to which belongs the prothallus in question, and, so far as can be judged, is almost median, the spore-walls being thus presented in true transverse section.

The spore-coat has dehisced, and the slit thus opened at the summit of the spore has been considerably widened by the expansion of the prothallus, so that a wide mouth is left, which is bridged by the ventral surface of the prothallus.

The spore-coat itself, although thick, is not of cellular composition, but is, in general, absolutely compact and opaque, being constructed of black, granular matter.

Borne upon its exterior, forming an equatorial belt, are numerous slightly-branched appendages, of the same dark colour as the spore-wall, and apparently of substance continuous with it. These appendages are short, being but little longer than the thickness of the spore-wall, and seem to have been invested by a dark membrane, which appears in longitudinal section on each side of several of them.

Appendages of the same kind, which are well known from many spores of similar character, occur in different forms and diversely distributed. They were originally described by Reinsch[1] as parasites of the spores, which latter he considered to be individual organisms, naming the supposed genus *Triletes*; the appendages he placed in a genus *Trichostelium*, belonging to a group called Stelideæ. There seems little reason to believe that this view is other than fantastic.

Apart from the equatorial belt, the exterior of the spore-coat is smooth; and the coat is of even thickness, save where there is

[1] Reinsch, J. P. "Micro-Palæo-Phytologia Formationis Carboniferæ," 1884.

an increase to form labial ridges on each side of the line of dehiscence, and a vague thickening somewhat further back than the labia, which seems to indicate a secondary ridge surrounding the mouth, whatever shape, tri-radiate or otherwise, that area may have been. On the inside, the surface layer of the spore-wall shows a tendency towards becoming detached from the main portion.

In seemingly identical spores, some of which have been found even in tetrad groups within a sporangial wall, the apex of the spore was produced into a long tubular thick-walled process, often twisted or flattened.

The general shape of the spore is rather like that of a tomato (of which the stalk would represent the apical prolongation of the spore) ; that is to say, the vertical section shows an oval outline, of greater breadth than height. In conjunction with this form, the development of an equatorial belt of ramenta must have rendered it inevitable that the shorter axis of the spore should remain vertical, and even suggests the possibility that the spore was intended to float, and to germinate upon the surface of water. The appendages on fossil megaspores apparently acted as collectors of the microspores, for, in many sections, these are found entangled among them in large numbers. The habit of germination while floating may account for the production of archegonia low down on the prothallus, as described below.

Within the cavity of the spore is an irregular bounding membrane, connected to the spore-wall at the two edges of the line of dehiscence, but otherwise free. The second membrane, represented darker in the figure, is most probably only a crack in the matrix, filled with some carbonaceous material.

The prothallus, which lies almost entirely outside the spore, is stretched across the open mouth, from lip to lip, and is in close contact with each. Although no doubt originally represented, in three dimensions, by a cushion of tissue, this section shows a bilobate outline, somewhat recalling the outline of a prothallus of *Aspidium*, or, more particularly, that of *Salvinia*, the base of the prothallus being in the mouth of the spore, and the lobes diverging outwards.

The prothallial tissue is formed of angular parenchymatous cells, rather elongated in a direction perpendicular to the surface of the prothallus, having thin, black walls, but with no contents preserved. The periphery is marked by smaller cells than those in

the interior, frequently containing dark material, while the central portion, which is sunk between the swelling lateral lobes, is badly preserved and full of dirt, so that its structure is difficult to make out.   Nothing which might be considered an apical cell is to be seen, but the cells of the centre are all smaller than those of the lobes.

The arched " ventral " surface, that turned towards the interior of the spore, does not seem, as preserved, to have been a surface during life, for its irregular nature suggests that the original surface has perished, and there are faint traces of tissue to be seen beneath it within the cavity of the spore, which increase this probability.

Sunken in the tissue of the prothallus, are preserved the vesicles supposed to represent the archegonia.   There are three which are more or less conspicuous, and two more doubtful examples, hidden in the dirt, which masks the central mass of tissue.

The three with which we are concerned show nothing of a neck, they represent merely the egg-cavities.   By means of experimentation on plasticine models, using the figures published by Gordon (see below) as a guide, it was possible to determine that the plane of the section lies at an angle of approximately 40% to the axes of the archegonia.   Consequently nothing is seen of the necks, save some indication in the shape of the vesicles as to where they were attached.   These vesicles are not surrounded by any special sheath, but are distinguished from the surrounding tissue only by their conspicuously larger size and thicker walls. They are so deeply sunken in the prothallus, and so remote from its surface, as represented in the plane of the section, that one is obliged to suppose their connection with the exterior world to have been in some other direction than in that plane.

One of those in the central region shows what may have been the base of its neck, indistinctly visible.   The vesicles vary in shape, the uppermost being somewhat longer than the others, but this may be due to variation in the direction along which the section cuts them, the latter being cut more longitudinally than the others.   The walls of all are deeply stained.   The way in which the lowermost is placed, with relation to the labia of the spore-coat, suggests that the whole prothallus has been pushed to some extent downwards into the spore-mouth during fossilization.

Below are given the measurements of the specimen :—

Spore. - Length - 1·86 mm.

Height - 1·38 mm.

Thickness of Wall - ·17 mm.

Width of Mouth - ·72 mm.

Prothallus. Length - ·76 mm.

Height - ·24—·38 mm.

Archegonia. Width - ·062—·08 mm.

A most striking feature of the preparation, is the development of rhizoid-like processes in the interior of the spore.

These are much branched-filaments, originating chiefly at the two points where spore-wall and prothallus meet, and filling the entire cavity of the spore with a mass of branches, there being many more present than have been represented in the figure (Plate VI). These filaments are doubtfully septate; but the presence of carbonaceous foreign matter round the filaments prevents any certainty about it. They seem to open into small vesicles, masked by dirt, at their points of origin.

Were these filaments absorbing organs of the prothallus or not ? If they were, does the specimen represent a type intermediate between a free living and an enclosed female prothallus ?

No absolute connection between the prothallus and any of these filaments can be traced, a fact which is a serious drawback to the affirmative view. If they are septate, they belong to an order of structure uncommon in present day plants, although septate rhizoids do occur in the Cyatheaceæ, and in *Danaea*.[1] They are very thin-walled and light in colour, agreeing in appearance with undoubted fossil fungus hyphæ. They present, among themselves, considerable differences in diameter, which would not be expected in short rhizoids, but is to be found in the old mycelia of some recent saprophytic fungi. Again, rhizoids are not often branched, more especially richly branched as these structures are, while this character agrees with the view of their fungal nature. Lastly, their apparent origin at the point of junction of prothallus and spore-wall is a suspicious character, for, were they intruding fungi, this is precisely the point at which entrance would have been easiest. It is true that no hyphæ are to be found in the surrounding matrix, but it is evident, from an examination of other specimens, that hyphæ were often preserved in the interior of spores (which they commonly enter at the point of dehiscence),

[1] Goebel. " Organography of Plants," II, p. 118,

and other organs, while completely destroyed outside. Even could all other objections be disposed of, there would still remain the difficulty of accounting for their production from a morphologically interior surface.

The weight of argument seems to be against viewing them as rhizoids of the prothallus, so that they may be dismissed as merely invading hyphæ, in spite of the attractiveness of the other theory. Intermediate stages between the free living Lycopod gametophyte, and the enclosed prothallus of forms like *Lepido-carpon*, there may, most probably, have been, and there is no reason why one such stage should not have presented an appearance analogous to this, with rhizoids developed almost entirely within the spore-coat. Some day such a stage may actually be found ; unless functional mutation took place suddenly from the free -form to the entirely enclosed, intermediate stages being passed over.

Our present prothallus, however, seems to represent a stage further in the reduction than the suggested hypothetical one, for it has no preserved rhizoids in the interior. Nevertheless, there still remain a few outside, as attested by little, tubular protuberances to be seen on one or two of the peripheral cells, which can only be the stumps of rhizoids.

Very few other fossil Lycopodineous prothalli, exclusive of *Lepidocarpon*—where the prothallus is not uncommonly found— have been described, and no specimen of that belonging to *Bothro-dendron* has previously been recorded. Scott in the " Studies in Fossil Botany "[1] has figured an irregular-looking megaspore of *Lepidostrobus Veltheimianus*, which is partly open and is filled with a regular, parenchymatous mass of cells, more or less isodiametric, but capped by a patch of small-celled tissue.

W. T. Gordon[2] has recorded two specimens, both belonging to the same species as that described by Scott, which has evidently been specially liable to good preservaton. In one of these, which appears to be a median vertical section, the spore is unopened, and presumably unripe. The interior is filled with a parenchymatous mass, as in Scott's specimen, but the lenticular cap of small-celled tissue is much better developed, and recalls the appearance of the gametophyte in *Selaginella*, although there are no archegonia. In

[1] Second Edition, 1908, Part I, p. 188, Fig. 77.

[2] Gordon. " Annals of Botany," Vol. XXIV, No. XCVI. Oct. 1910 " Transactions of the Botanical Society of Edinburgh." and Vol. XXIII, 1908.

his second specimen only a matured archegonium and a few adjacent cells are preserved, but the specimen is of great interest. The neck of the archegonium, consisting of three rows of cells, also the internal cells, are excellently displayed.

Lepidostrobus Veltheimianus seems, therefore, to have been of a type more reduced than the present example, as the archegonial layer of tissue is developed only in the mouth of the spore, not extruded from it as in the present instance, and also because the neck of the archegonium is reduced in length.

Renault[1] has also described imperfectly preserved prothalli from undetermined megaspores of *Lepidostrobus*, and the fine prothallus recorded by Dr. Margaret Benson in the megaspore of *Mazocarpon* is well known.[2] The large irregular masses of " cells " sometimes found inside megaspore walls, and labelled "prothalli" are more probably merely mucilaginous vesicles formed by the breakdown of the previously-contained reserve material.

The uncommon position of the prothallus here described,
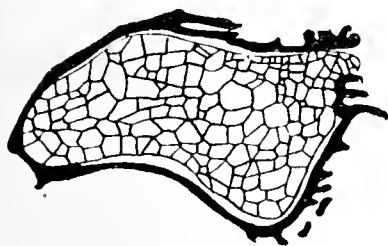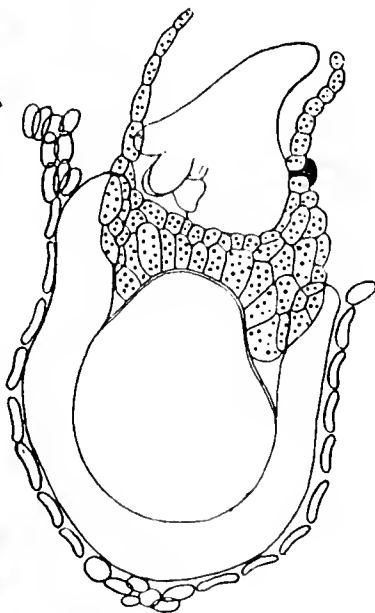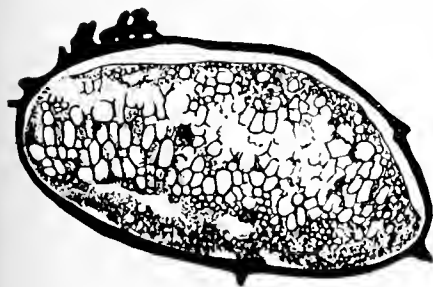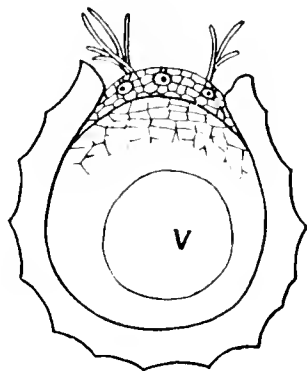
Text-Fig. 2.

A. *Lepidostrobus veltheimianus* : prothallus. After Mrs. D. H. Scott. ×20.

B. *Mazocarpon* : immature prothallus. After Dr. Margaret Benson. ×24.

C. *Salvinia natans* : embryo in prothallus, which is situated in the open mouth of the spore. After Pringsheim. ×66.

D. *Selaginella* : mature prothallus, with beginning of segmentation of food material within spore. V=vacuole. ×66.

[1] See Lotsy. " Botanische Stammesgeschichte," II. p. 458.

[2] See Scott. " Studies in Fossil Botany." 2nd Edition, Part I, p. 189. Also Benson, " The Sporangiophore" NEW PHYT., Vol. VII, Nos. 6 and 7, 1908.

exterior to the spore, and resembling strongly the position of the corresponding organs in such Hydropterideæ as *Pilularia*, can only have been attained, if the mature structure was developed from a small cap of cells, by the upward pressure of a mass of material originally occupying the interior of the spore (whether undifferentiated, plasmatic reserve-material, or a firm cellular tissue), and further, by continued growth in thickness of the original cell-cap, until the protruding cushion was produced.   There is a distinct presumption, from analogy with corresponding specimens, that the whole interior was actually cellular in nature, but this cell-structure has disappeared, possibly subsequent to the invasion by fungus hyphæ.

In Text-fig. 2 are shown some other similar prothalli for purposes of comparison.

Salvinia in younger stages shows the lobate outline of the present specimen.   *Mazocarpon* cannot be very well taken into comparison, as it has never been described in a fully developed condition.

The figure given by Gordon of the prothallus of *Lepidostrobus Veltheimianus* in the Trans. Bot. Soc., Edinburgh, 1908, resembles in general character that of *Mazocarpon* figured above.   *Isoëtes* on the other hand is more reminiscent of *Selaginella*.

To sum up, it may be said that this specimen represents a stage in the reduction of the primitive free-living Lycopod gametophyte, toward the condition obtaining in the " seed " of *Lepidocarpon*.   The prothallus was not produced until after the megaspore had been shed. It developed outside the spore, but remained attached to the spore-wall at its base, and in form resembled the prothalli of modern heterosporous ferns.

The gametophyte of *Bothrodendron* was then more primitive than that of *Lepidodendron*, where the archegonia developed inside the spore.

My best thanks are due to Professor F. W. Oliver, F.R.S., who suggested this description for the use of both the above specimens and for his kindness in revising the manuscript ; also to Professor A. C. Seward, F.R.S., for much kind interest and information ; and to Mr. D. S. Watson for his identification of the spore.

Plates V and VI, illustrating this paper, are reproduced in photogravure, from burnt umber drawings by the author, by the Swan Electric Engraving Company, Ld., and represent with extreme faithfulness both the form and the colour of the original sections.

ON THE INFLUENCE OF THE STRUCTURE
OF THE ADULT PLANT UPON THE SEEDLING.

By T. G. Hill and E. de Fraine.

[With 3 Diagrams and 9 Text-Figs.]

IN much, if not in all, of the recent investigations upon the anatomy of seedlings, the influence of the general morphology of the adult plant—which mainly depends upon physiological necessity—upon the seedling has not been appreciated.

That such an influence is exerted cannot, we think, be denied ; although, naturally, it is only by the study of those plants shewing marked peculiarities that the phenomenon is at all conspicuous. And not only may the characteristic external morphology be thrust back, as it were, into the seedling—that is into the embryo—but the same holds for anatomical peculiarities.

To take a few examples: in *Convolvulus tricolor* and in certain Solanaceæ, *Datura Stramonium* for example, plants in which the vascular cylinders of the epicotyledonary axes are characterized by medullary (intraxylary) phloem, it is found that in the cotyledons and hypocotyls this same peculiar anatomical character obtains.

In *Mirabilis*[1] there are similar points of correspondence in anatomical details: a characteristic feature of the stem-structure of the adult is the polycyclic arrangement of the vascular bundles, some of which may be bicollateral or even concentric; the hypocotyl exhibits similar phenomena.

Salicornia,[2] as is well known, has a very distinctive appearance. The succulence of the stem of this plant is due not to cortical tissue, but to the foliage, the basal portions of which form decurrent sheaths around the axis. Almost exactly the same thing is found in the seedling; the cotyledons are very small and fleshy, and fuse laterally to form a tube the base of which is decurrent down the hypocotyl, thus forming the so-called succulent " cortex." Further, the distribution of the leaf-traces is the same in the adult and in the seedling: to each leaf, or cotyledon, a single vascular bundle passes out from the node and branches into three; of these, the median strand supplies the tip, whilst the two lateral bundles curve outwards and pass downwards, their branches supplying the

[1] Hill and de Fraine. On the Seedling Structure of Certain Centrospermæ. Ann. Bot., 1912, XXVI.

[2] Hill and de Fraine, *loc. cit.*

sheath and, ultimately, ending blindly in the aqueous tissue. Nothing comparable to these facts has been observed in any of the other Centrospermæ examined.

The Cactaceæ provide similar instances. It was shewn some years ago by Ganong[1] that the form of the seedling corresponds very closely with that of the adult plant. The study of the seedling structure has shewn that this assumption of the adult habit has had a profound influence upon the seedling anatomy.[2]

In the leafy forms, e.g., *Pereskia, Opuntia* and *Nopalea,* the sequence of events in the transition-phenomena is reasonably straight-forward, the *Anemarrhena*-type being dominant; but in those which have a succulent seedling the transition is very variable. Type 3 is the one followed, but the details vary considerably according to the morphology of the seedling; for the cotyledons, as such, may not be present, so that the vascular supply of other members plays the prominent part in the phenomenon. In *Echinopsis* the behaviour of the seed-leaf-traces depends almost entirely upon the degree of development of the vascular supply of the tubercle. Thus when the tubercle is well differentiated its bundles may play the more important part in the transition-phenomena.

Similarly in *Mamillaria pusilla,* which has no cotyledons, the epicotylar strands assume the part normally played by the cotyledonary traces in the transition.

These and similar facts shew the important influence which morphology, and consequently physiology, exerts upon the structure and gives much weight to the view that in many cases anatomical detail is of no value in determining phylogeny.

The examination of *Persoonia lanceolata* forms the coping stone, as it were, to our thesis—the influence of the adult structure upon the seedling.

The Seedling-Anatomy of *Persoonia lanceolata,* Andr.
(N. O. Proteaceæ).

Our attention was first drawn to the seedlings of the Proteaceæ by the publication of the interesting results obtained by Fletcher.[3]

[1] Ganong, W. F. Contributions to a Knowledge of the Morphology and Ecology of the Cactaceæ II—The Comparative Morphology of the Embryos and Seedlings. Ann. Bot., 1898, XII.

[2] de Fraine, E. The Seedling Structure of Certain Cactaceæ. Ann. Bot., 1910, XXIV.

[3] Fletcher. Illustrations of Polycotyledony in the genus *Persoonia,* with some reference to *Nuytsia.* Proc. Linn. Soc., New South Wales, 1908, XXXIII, Pt. 4.

As is well known the Proteaceæ are remarkable in several respects; on the present occasion it is desired only to mention a few of their peculiarities, *viz.*, their xerophytic habit, their general vegetative resemblance, in some cases, to certain Gymnosperms and the occurrence of polycotyledony.

Fletcher especially investigated, from the point of view of external morphology, this last phenomenon and came to exactly the same conclusion as the present authors with regard to the origin of polycotyledony, *viz.*, by the splitting of two original structures.[1]

The resemblance in the habit of certain Proteaceæ and Gymnosperms is sufficiently well shewn by Figures 1 and 2 which represent well-developed seedlings of *Persoonia pinifolia*, R.Br. and *Pinus sylvestris*, L. respectively.

A seedling of *Persoonia lanceolata*, of roughly corresponding age,

FIG. 1. A seedling of *Persoonia pinifolia* with seven cotyledons; some of the lowest foliage leaves were removed to expose the cotyledons. About nat. size. (After Fletcher).
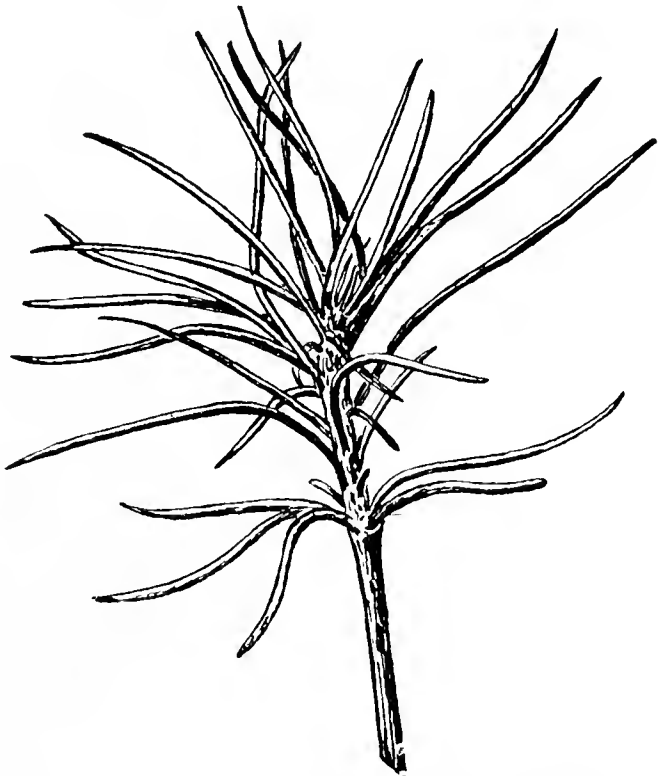
FIG. 2. A seedling of *Pinus sylvestris*, not developed quite so far as the plant shewn in Fig. 1, and shewing six cotyledons. × about 2.

is illustrated in Figure 3. It will be observed that in this plant the resemblance to the gymnospermous habit is confined chiefly to the cotyledons, a feature which stands out more clearly if younger seedlings be examined. Three such are shewn in Figure 4, one with three cotyledons and two others, in whieh the upper regions only

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[1] Hill and de Fraine. On the Seedling Structure of Gymnosperms. II—Ann. Bot., 1909, XXIII.

are represented, shewing the origin of a fourth seed-leaf by the splitting of a single cotyledon. Of these two seedlings, one shews the bifurcation not far advanced, whilst in the other the splitting has extended almost to the base. The resemblance to seedlings of certain Cupressineæ is well marked,
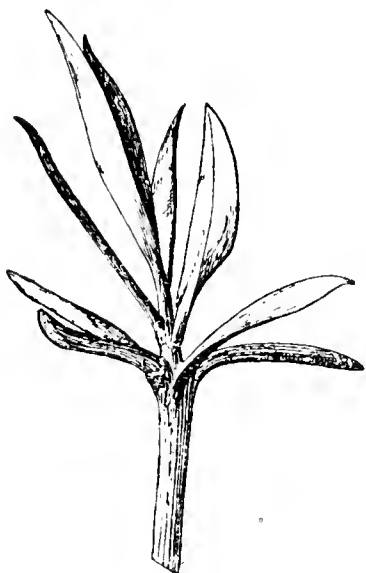
FIG. 3. A seedling of *Persoonia lanceolata* with four cotyledons. About nat. size. (After Fletcher).
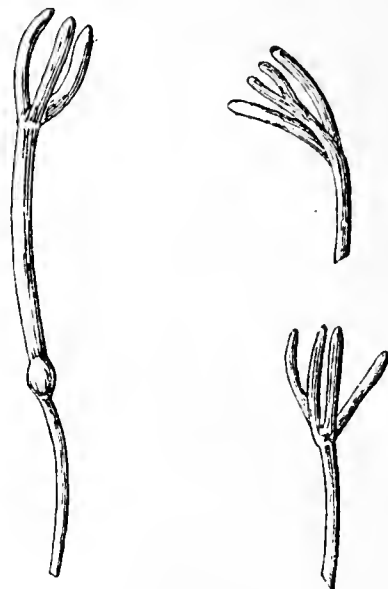
FIG. 4. Three young seedlings of *Persoonia lanceolata*. About nat. size.

At the base of the hypocotyl of the seedling with three cotyledons represented in Figure 4, a distinct swelling is seen ; whether this is general we are unable to say : it is, however, without effect on the details of structure.

No. of Cotyledons.	*Persoonia lanceolata.*[1]		*Persoonia pinifolia.*[1]		*Pinus sylvestris.*[2]	
	No. of Seedlings	Per-centage.	No. of Seedlings	Per-centage.	No. of Seedlings	Per-centage.
3	84	28	...	...	2	·2
3 (1 bipartite)	10	3·3 ⎱ 3·6	...	...	...	...
3 (2 ,,)	1	·3 ⎰	...	...	...	...
4	186	62 ⎱ 64·3	4	3·3	28	3·0
4 (1 bipartite)	7	2·3 ⎰	...	...	...	...
5	12	4	52	42·6 ⎱ 44·2	171	18·1
5 (1 bipartite)	...	...	2	1·6 ⎰	...	...
6	...	...	47	38·6 ⎱ 42 7	500	53·0
6 (1 bipartite)	...	...	5	4·1 ⎰	...	...
7	...	...	12	9·8	209	22·1
8	...	...	...	...	34	3·6
	Tot. 300		Tot. 122		Tot. 944	

[1] Fletcher: *loc. cit.*

[2] Hill and de Fraine : Gymnosperms, Pt. 2, *loc. cit,*

The number of seed-leaves in these plants varies; Fletcher, in the case of *Persoonia lanceolata*, found the range to be between three and five. Although we have not had the opportunity of examining *Persoonia pinifolia*, *P. lanceolata* being the only species available for our investigation, some figures relating to the variation in the number of the cotyledons of the former plant may be quoted, since we have used it as a basis for comparison (Table p. 322).

It will be observed that the range is somewhat wider in *P. pinifolia* than in *P. lanceolata*, but not quite so wide as in *Pinus sylvestris*.

In the paper referred to, Fletcher gives further examples of a similar kind. It is thus seen that the Proteaceæ in their poly-cotyledony closely resemble many Gymnosperms, more especially those with acicular leaves; and this suggests that marked poly-cotyledony may possibly be connected with this particular coniferous form of xerophily.

STRUCTURE OF THE COTYLEDONS.

The resemblance to certain Gymnosperms is, perhaps, even more striking when the internal structure is examined. The fleshy cotyledons are covered with a well-defined cuticle, the epidermis is quite normal, but the stomata, which are flush with the general level of the surface, are characterised by the presence of two sub-sidiary cells, one on each side of and parallel with the guard-cells. This is a feature which we have not observed in any Gymnosperm.

The mesophyll of *Persoonia* does not shew much differentiation; in young cotyledons and in the more apical parts of older ones the mesophyll consists of undifferentiated parenchyma; but in the middle and basal regions, the peripheral cells may shew a certain amount of radial elongation so that the chlorenchyma may be more or less clearly differentiated into palisade and spongy parenchyma. This, possibly, may be more strongly marked in old seed-leaves. The chlorophyll-containing cells of the cotyledons, as also in Gymnosperms, have not the internal flanges characteristic of the adult foliage of many Coniferæ and also some Proteaceæ, e.g., *Persoonia juniperina*; nor are resin ducts present, a feature, it will be remembered, not at all general in the cotyledons of Gymno-sperms at large.

Each seed-leaf of *Persoonia lanceolata* is traversed by a single vascular strand, a point of resemblance to many Cupressineæ and Abietineæ; it must, however, be remarked that in some cases the bundles of the cotyledons of *Persoonia* do shew a tendency to

branch, small portions becoming more or less detached from the flanks of the central bundle. This separation, however, when it does take place, is merely local; in no case have two distinct bundles been seen.
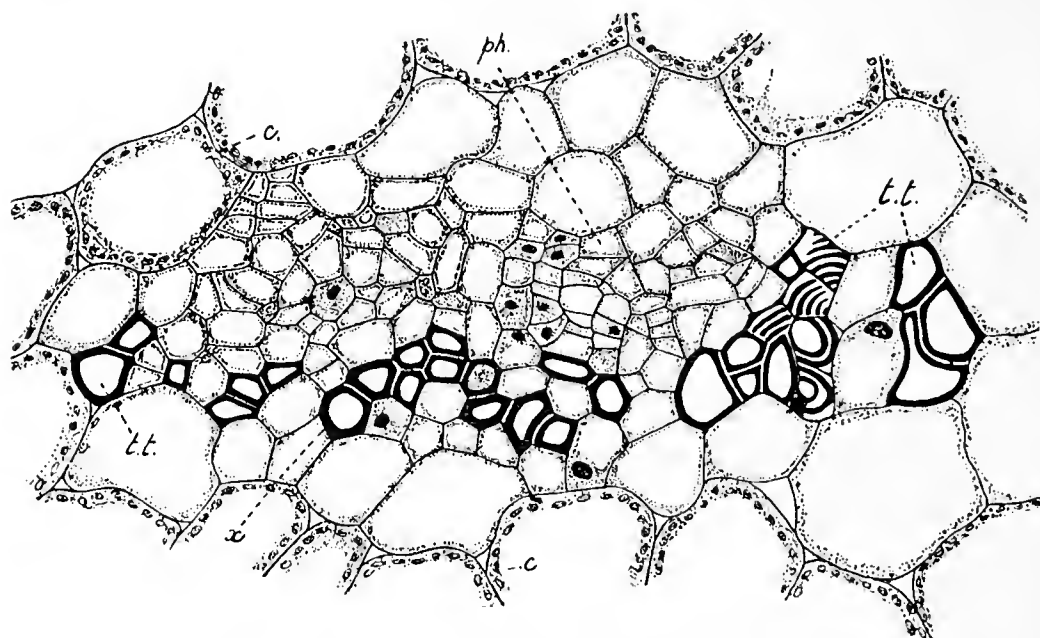
FIG. 5. *P. lanceolata.* Transverse section of cotyledon shewing details of structure of the vascular bundle ; *c.*, chlorenchyma ; *ph.*, phloem ; *t.t.*, transfusion tracheides ; *x.*, xylem.   The transfusion tracheides are particularly abundant on the right flank.   × 280.
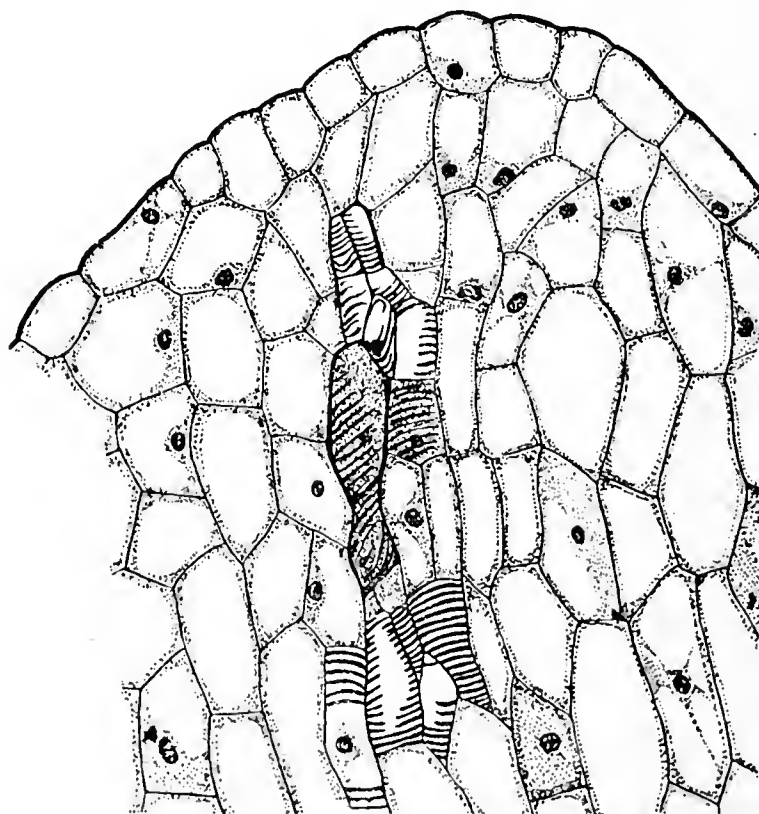
FIG. 6. *P. lanceolata.* Longitudinal section of a cotyledon, shewing the transfusion tracheides reaching almost to the tip.   × 200.

With regard to histological details the bundles have a general gymnospermous appearance, the xylem being composed of narrow tracheæ, which shew but little variation in size ; the phloem, however, is fairly distinct (Fig. 5). The great point of resemblance is found in the presence of transfusion tracheides in *Persoonia.*
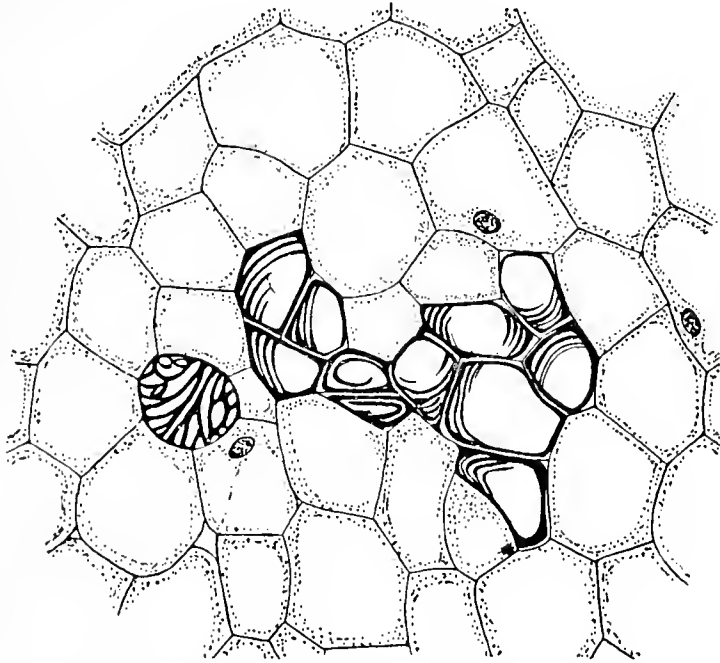
FIG. 7. *P. lanceolata.* Transverse section of a cotyledon cut just behind the apex, shewing the transfusion tracheides. × 280.

These elements are found in greater or lesser abundance throughout the whole length of the cotyledon generally in proximity to the vascular bundle ; they extend almost to the apex of the seed-leaf (Figs. 6 and 7), further than the vascular bundle, where they may pass outwards from their central position to within one or two cells of the epidermis (Fig. 8). This lateral extension varies ; in some cases there may be a more or less continuous chain of trans-usion elements, as shewn in Fig. 8, or, in other cases, small groups of these cells may be scattered in the mesophyll towards the periphery.

On passing downwards from the apex of a seed-leaf, the trans-fusion tracheides are seen to join, more or less completely, with the xylem of the vascular bundle ; and at this level, or just below, there is generally a diminution in their number, at any rate for a short distance.

In the lower regions these particular cells are most marked on the flanks of the bundles, where as many as ten may form a con-spicuous group (Fig. 5): the number, as was to be expected, varies considerably in sections taken from different levels.

The transfusion tracheides, however, are not restricted to the

sides of the vascular strands: although commonly they extend outwards as far as the lateral limits of the phloem, they may extend further (Fig. 5) and also may occur on the dorsal and ventral sides of the bundle (Figs. 9, 10 and 11).

In one seedling transfusion tracheides were found in the mesophyll well towards the periphery of the cotyledons and forming an interrupted zone of groups of cells extending about half-way round the circumference of the seed-leaf. These cells always retained their isolated position: in no case were they seen to become connected by similar elements with the vascular bundle. It is thus seen that the transfusion-tracheids in *Persoonia* corresponds to what obtains in many Gymnosperms.[1]

Incidentally it may be mentioned that the transfusion tracheides of *Persoonia* are not restricted to the cotyledons: they may occur in the upper region of the hypocotyl and in the foliage leaves of *Persoonia lanceolata* and *P. juniperina*.

FIG. 8. *P. lanceolata.* Transverse section near tip of cotyledon. Transfusion tracheides are seen extending towards the periphery. × 335.

The elements in question arise in no very definite order, as is shewn by the irregular appearance of immature tracheides amongst mature dead ones. Thus, in Figure 6, whilst those at the apex are mature, some lower down, shewing rather indefinite thickenings and containing protoplasm and nuclei, are immature. Again in Figure 9, immature elements occur with adult ones on the flanks of the bundle.

The size of the transfusion tracheides varies: at the apex of the seed-leaf (Figures 6, 7 and 8) their dimensions, as viewed in

See Bernard : Le bois centripète dans les feuilles de Conifères. Beih. Bot. Centrbl., 1904, XVII.

Daguillon : Recherches morphologiques sur les feuilles des Conifères. Rev. Gén. Bot., 1890, II.

Hill and de Fraine : Seedling Structure of Gymnosperms, I, II, and IV. Ann. Bot., 1908, XXII ; 1909, XXIII ; 1910, XXIV.

transverse section, are roughly the same as those of the parenchyma of the surrounding mesophyll; at lower levels, however, the size is
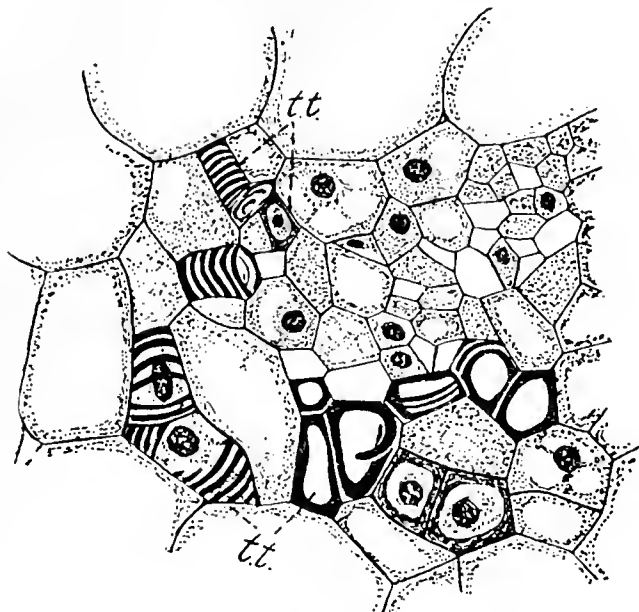
FIG. 9. *P. lanceolata.* Transverse section of cotyledons, shewing one side of bundle. Mature and immature transfusion tracheides (*t.t.*) are seen. × 355.

more variable (Figures 5, 9, 10 and 11). The examination of longi tudinal sections shews a closer correspondence between the lengths of the transfusion tracheides and parenchyma : this is shewn in Figure 12.
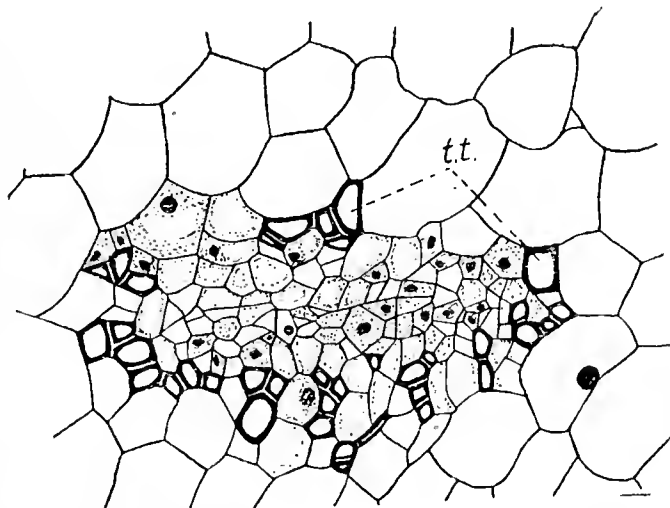
FIG. 10. *P. lanceolata.* Transverse section of a seed-leaf, shewing trans- fusion tracheides (*t.t.*) on the flanks and on the dorsal side of the bundle. × 200.

As far as has been seen the thickening of the elements in question is either annular or spiral; in no case have bordered pits, which are characteristic of the transfusion tracheides of many Coni- feræ, been observed. It will, however, be remembered that there is much variation in this respect in the Gymnosperms; although they are pitted in *Pinus*, they are annular or spiral in *Podocarpus*

chinensis and *Ephedra distachya*, and spiral and pitted in *Sciadopitys verticillata*, etc.[1]
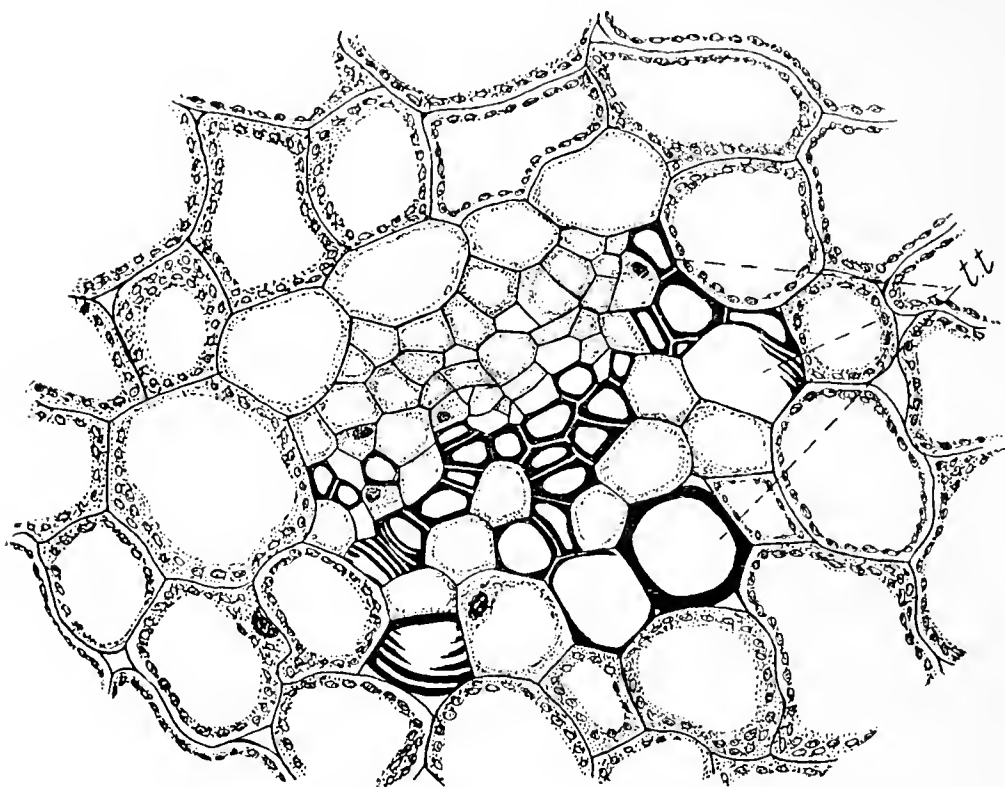
FIG. 11. *P. lanceolata.* Transverse section of cotyledon, shewing transfusion tracheides (*t.t.*) on the flanks and ventral side of the bundle. × 335.

With regard to the function of the transfusion tracheides much cannot be said owing to the paucity of experimental data; it is, however, reasonable to suppose that they convey water from the vascular bundle to the surrounding mesophyll. At the same time they may be of value in storing water, a function which is suggested by their not infrequent isolated position, and they are thus comparable to the barrel tracheides of certain Cactaceæ.

The close resemblance in the structure and position of the transfusion tracheides of *Persoonia* and many Gymnosperms gives weight to the view[2] that in the latter plants the elements in question may have no connexion with centripetal wood, but are structures brought into being at the call of physiological necessity.

TRANSITION.

The transition-phenomena exhibited by *Persoonia lanceolata* follow those of Van Tieghem's Type 3, which is so well known that the briefest description only is required.

In the plant in question each cotyledon normally has a single vascular bundle which usually remains endarch and collateral

[1] See Bernard, Daguillon, and Hill and de Fraine, *loc. cit.*

[2] See Carter: A Reconsideration of the Origin of Transfusion Tissue. Ann. Bot., 1911, XXV.

throughout the whole length of the seed-leaf. In a very few cases the phloem may divide into two masses in the base of the cotyledon ; it is, however, in the upper region of the hypocotyl that each seed-leaf-trace divides completely into two, each half rotating in such a way that the protoxylem becomes isolated and bounded on each side by metaxylem and phloem elements. In this process a certain amount of variation may obtain : generally the bifurcation of the bundle and the rotation of its two halves is well-marked and takes place in a short vertical distance ; in such cases the protoxylem takes up its exarch position, and, as it were, moves outwards very quickly. On the other hand, it sometimes happens that the protoxylem remains relatively stationary so that the assumption of the exarch position is much slower and is arrived at rather by the rearrangements of the other vascular tissues.

Finally the corresponding metaxylem and phloem groups fuse together so that the root-structure is organized in the upper part of the hypocotyl.

In a normal plant the number of poles in the root will obviously cor-

Fig. 12. *P. lanceolata.* Longitudinal section of a cotyledon shewing parenchyma (*par.*), phloem (*ph.*), protoxylem (*px.*), and transfusion tracheides (*t.t.*). × 280.

respond to the number of cotyledons, but when polycotyledony obtains, this number may be less than that of the seed-leaves. This is especially the case in the Coniferæ, and the study of the behaviour of their cotyledonary traces has led to the classification of their seed-leaves into whole-cotyledons, half-cotyledons, and subsidiary cotyledons.[1] Also it is very general to find that the number of leaves in the first foliage-whorl and the number of cotyledonony buds, when present, correspond to the equivalent of the number of whole-cotyledons.

[1] Hill and de Fraine : Gymnosperms II, *loc. cit.*

As the transition-phenomena obtaining in the polycotyledonous *Persoonia lanceolata* are parallel with those of Coniferæ a brief analysis only is required.

1. *Seedlings with three cotyledons and a triarch root* (series A, B and C).

Three examples were examined and in all the vascular bundles of each seed-leaf organized one pole of the triarch root-structure. Each seed-leaf may therefore be considered as a whole-cotyledon.

2. *Seedlings with four cotyledons and a tetrarch root* (series D, E and F).

The details of the transition were exactly the same as in the previous series. Each seed-leaf corresponds to a whole-cotyledon.

3. *Seedlings with four cotyledons and a triarch root.*

Series G. This seedling formed a transition between the two previous groups, for one cotyledon was split almost entirely into two halves (Diagram 1, Figure 1), and was traversed by two vascular bundles which remained distinct one from the other throughout the whole length of the cotyledon (Diagram 1, Figure 1, *a* and *b*). Within the hypocotyl these two strands together organized one pole of the triarch root (Diagram 1, Figures 2, 3 and 4): on the other hand the bundles of the other seed-leaves (Diagram 1, *c* and *d*) behaved quite normally and are therefore classed as whole cotyledons. This seedling thus provided an example which shews the origin of two seed-leaves by the longitudinal fission of one.
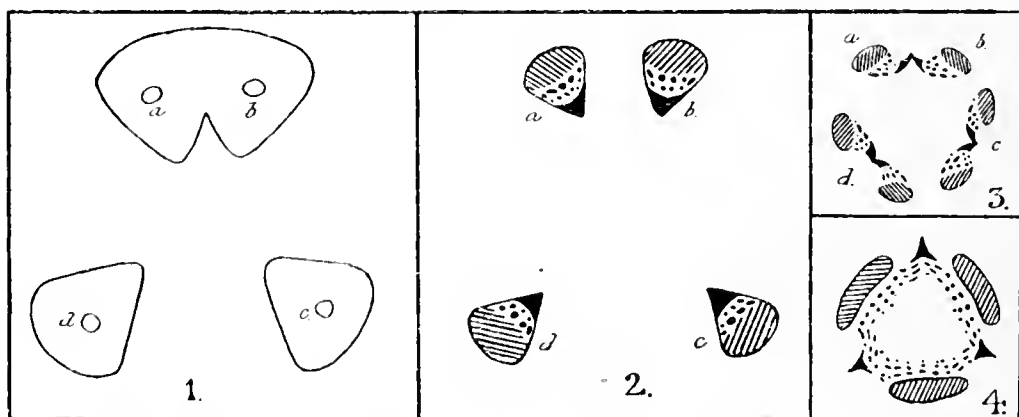
DIAGRAM 1. *Persoonia lanceolata*, series G. In this and in the two following diagrams, the protoxylem is indicated by black areas, the metaxylem by round or oval black dots and the phloem by shading.

Series H. This seedling resembled the previous one very closely, with the exception that one cotyledon had entirely divided into two; the vascular strands of the two half-cotyledons, in the upper region of the hypocotyl, rotated towards one another and together formed one pole of the triarch root-structure. The bundles of the other seed-leaves behaved in a normal fashion (Diagram 1,

Figures 2, 3 and 4). The four seed-leaves are thus made up of two whole-cotyledons and two half-cotyledons.

Series J. This seedling was found to be somewhat abnormal. Two of the four seed-leaves fused together just above the cotyledonary node, so that it was expected that they would fall into the category of half-cotyledons. It was found, however, that the bundle of one bifurcated and formed one pole of the root-structure, whilst the strand of the other, together with that of the adjoining seed-leaf, formed one of the other poles of the triarch root, the remaining pole being organized from the vascular tissue derived from the fourth cotyledon. There were thus two whole-cotyledons and two half-cotyledons.

Series K. Two of the cotyledons fused together just above the cotyledonary node, the others quickly did likewise so that a short cotyledonary tube was formed (Diagram 2, Figures 1 and 2). Of the seed-leaf bundles, three organized the three poles of the triarch root (Diagram 2, *a*, *b* and *c*) whilst the fourth (*d*) played no part in the transition. There were thus three whole-cotyledons and one subsidiary cotyledon.
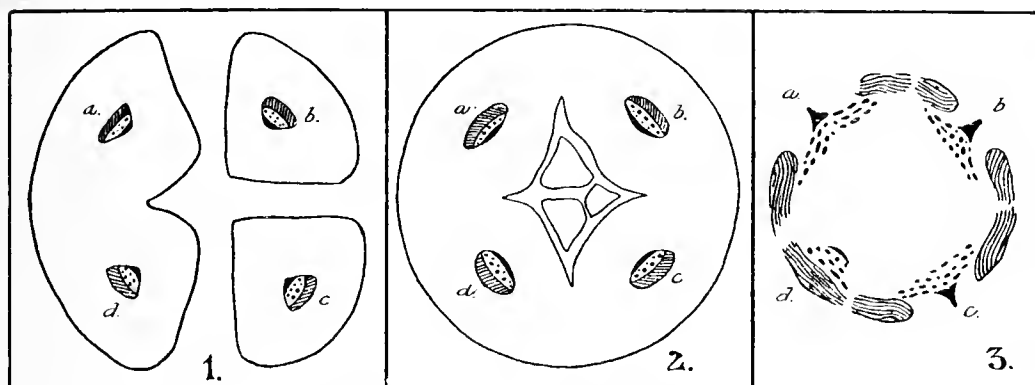
DIAGRAM 2. *Persoonia lanceolata*, series K.

4. *A seedling with five cotyledons and a diarch root.*

Series L. From the number of cotyledonary buds and of leaves in the first foliage whorl it was anticipated that a triarch root-structure would be formed. This, however, was not the case. The root was diarch from the first, a transient triarch structure not being passed through.

One cotyledonary strand (Diagram 3, *b*) bifurcated and rotated in the normal fashion; the bundles *a* and *c*, which were without influence in the transition, joined on to the adjacent halves of *b*; and the strands *d* and *e* rotated towards each other and together organized the remaining pole of the diarch root.

It is seen, therefore, that *b* corresponds to a whole cotyledon, *d* and *e* to half cotyledons, whilst *a* and *c* are subsidiary. This classification, however, is not quite satisfactory with regard to *a*

and *c*, since their protoxylems became continuous with that of *b* and thus contributed to the diarch plate.
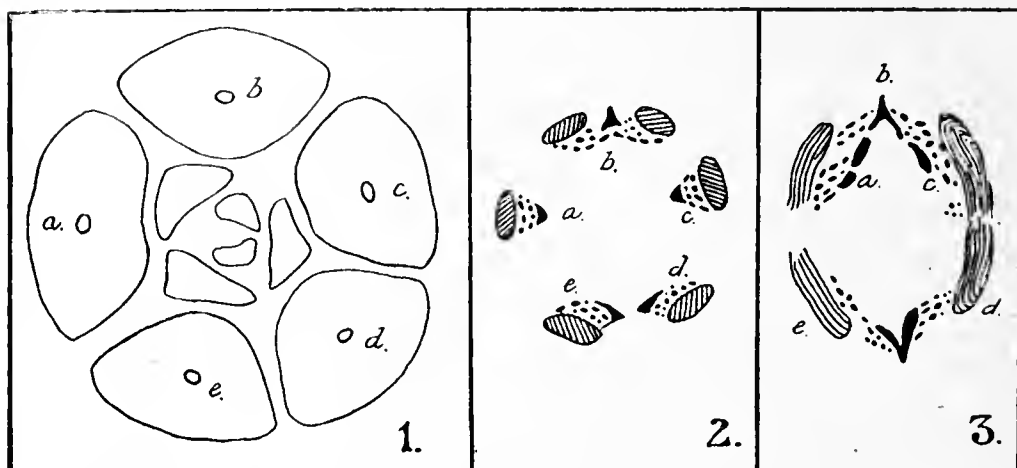
DIAGRAM 3.   *Persoonia lanceolata,* series L.

The following table summarizes the relationship between the cotyledons, poles of the root, etc.

Series.	No. of Cots.	Analysis of Cotyledons.			No. of Coty. Buds.	No. of leaves in first foliage whorl.	Root.
		Whole-Cots.	Half-Cots.	Sub-Cots.			
A, B, C	3	3	0	0	3	3	3-arch
D, E, F	4	4	0	0	0[1]	4	4-arch
G, H, J	4	2	2	0	3	3	3-arch
K	4	3	0	1	0[1]	3	3-arch
L	5	1	2	2	3	3	2-arch

[1] The cotyledonary buds were not developed in all cases.

This general survey of the seedling structure of *Persoonia lanceolata* is sufficient to indicate the close resemblance to the polycotyledonous Gymnosperms ; a resemblance which is found not only in the general morphological configuration but also in certain histological details and in the transition-phenomena, although the last, in *Persoonia*, are not, perhaps, quite so precise as in many Coniferæ.

It is, probably, quite unnecessary to state that we do not attach any phylogenetic significance to the similarities described ; the resemblance remarked upon is considered as a striking instance of homoplasy in which the adult has influenced to a considerable extent the seedling. This is of some importance since it is not at all unlikely that details of seedling-structure which might be used as a proof of a phylogenetic connexion between different classes of plants might be due to similar phenomena. These are matters, however, which we hope to consider at length on a future occasion.

In conclusion, we desire to express our warmest thanks to Mr. Fletcher for his kindness in sending us material.

UNIVERSITY COLLEGE, LONDON.
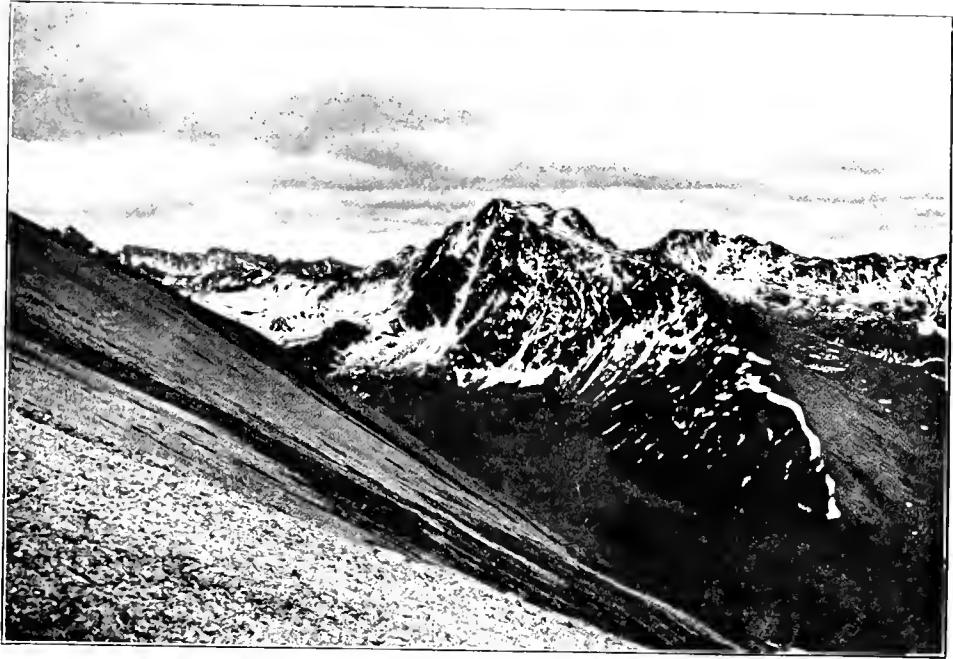
Fig. 1.

Fig. 2.
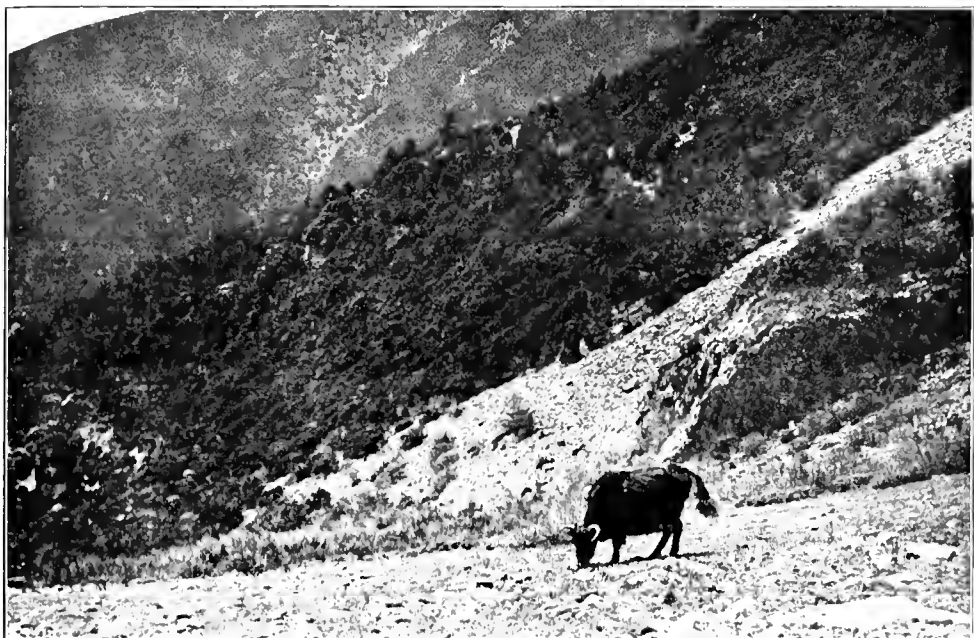
Fig. 3.
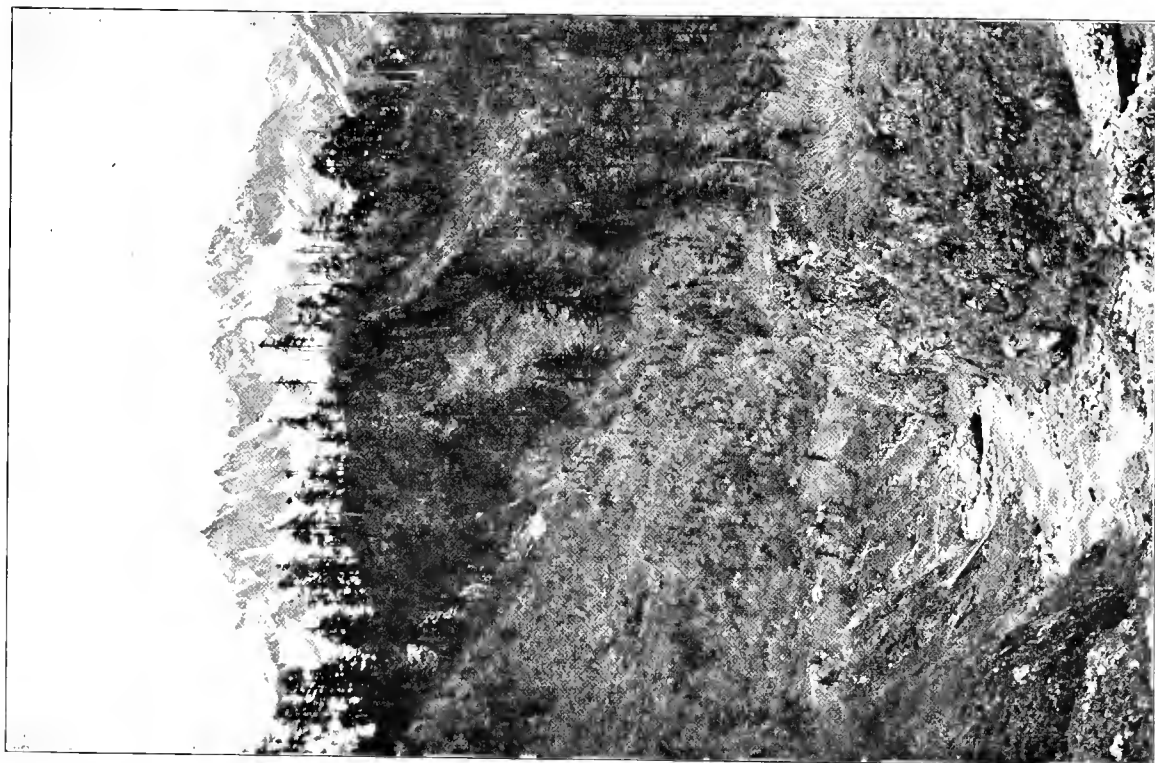
KINGDON WARD   LIMITS OF PLANTS IN N.W. YUN-NAN.

Fig. 2.

Fig. 1.

KINGDON WARD — LIMITS OF PLANTS IN N.W. YUN-NAN.

ON THE ALTITUDINAL LIMITS OF PLANTS IN NORTH-WEST YUNNAN.

BY F. KINGDON WARD, B.A., F.R.G.S.

[WITH PLATES VII AND VIII,

AND A MAP AND SECTION IN THE TEXT].

———

AN observant traveller mountaineering in N.W. Yunnan must inevitably be struck by the apparently capricious manner in which the vegetation changes its character, or ceases abruptly, now at one altitude, now at another. These transitions, however, do not really take place in the whimsical manner which at first sight appears, and in the following notes I will endeavour to point out some of the controlling factors which seem to me of chief importance in determining the formations, particularly as regards the extreme limits of flowering plants in these mountains.

My observations, being very incomplete, are necessarily supplemented by several suggestions which will doubtless be more or less open to criticism amongst those who have studied these problems.

The peculiar topographical features of the country favour peculiar climatic conditions, which, owing to the great variations of altitude condensed into a comparatively small area, exhibit both a wide range and abrupt transitions.

The country under review comprises three deep gorge-like valleys separated by two narrow mountain-chains, their axes of uplift trending north and south, their highest summits rising to an altitude of perhaps 23,000 feet; both ridges indeed rise well above the snow-line, and in this region exhibit a conspicuous chain of snow-clad peaks, though their average altitude is considerably less than that indicated (map p. 334).

The country is watered by the south-west monsoon blowing over the plains of Assam from the Indian Ocean, and deluging this part of Asia during the summer months; consequently we find a progressively diminishing rainfall from west to east, as I observed both from personal experience in the Salween, Mekong and Yangtze valleys respectively and by a comparison of the flora on the inter-vening ridges. Moreover a geologist would arrive at precisely the same conclusion by comparing the peaks of the two ranges, for while those on the Salween side shew the curved outline characteristic of water erosion (Pl. 8, Fig. 2), the crest of the watershed on the Yangtze side is capped by extraordinary towers and pinnacles, plainly the work of dry denuding agents (Pl. 7, Fig. 1); indeed the only two snow mountains I saw there were massive flat-topped buttresses not unlike the " nunatacks " of the Arctic, whereas the peaks of the Mekong-Salween watershed are most commonly pyramids.

Also, the rains begin earlier on the westernmost ridge than on those further east, since the first of the monsoon precipitates itself on the great bluff overlooking Assam before crossing the subsequent divides.

The great altitude of the Salween-Mekong divide in this region, and the consequent terrific rainfall it receives (for its peaks rise higher than any of those further west) determine a comparatively low snow-line, which stands at about 16,000 feet. And then comes a change.

The great bulk of the rain falls west of the Mekong, the ridge just referred to forming an effective rain-screen to the Mekong-Yangtze divide further east. The small precipitation it receives in consequence, and the magnificent autumn weather it enjoys, rapidly melting the snows of late summer, sufficiently accounts for the enormously elevated snow-line on the Mekong-Yangtze divide—I believe it to be hardly less than 19,000 feet. When we consider that there is eternal snow in New Guinea at 15,000 feet, the significance of this may be appreciated; it proves how little mere altitude affects the snow-line.

Sketch-Map to Illustrate Part of the Country Traversed.

Three high mountain ranges run north and south, and of those the western and the central act as rain-screens from the S.W. monsoon. The three main rivers, represented by double lines, run from south to north. The line of stars separates the arid from the rainy regions. The arrows show the directions of the winds and rivers. The writer's route is indicated by a dotted line accompanying a continuous line.

Unfortunately I was unable to proceed west of the Salween, but from above that river I obtained splendid views of the ridge separating the Salween from the 'Nmai-kha (the eastern branch of the Irrawaddy) capped both in June and November by a string of snow-clad peaks which evidently received the full force of the monsoon rains.

The Salween ridge is far more densely forested than is the Yangtze ridge, and presents several formations, such as *Alnus* forest, and high alpine meadow, not represented at all on the latter; but the composition of the forest on the two ridges presented, so far as I was able to judge, much greater differences than did the alpine flora, a fact doubtless to be attributed to the greater relative importance of rain to forest-land than to grass-land.

A traveller crossing from the Yangtze to the Salween during the summer would inevitably pronounce the flora of the Salween ridge to be far the richer of the two ; nevertheless I do not think he would be correct. Richer it emphatically is in individuals, as also in genera, but this is compensated for by the circumstance that the genera which occur on the Yangtze ridge are far richer in species.

Moreover, as already remarked, the rains break earlier on the Salween ridge than on the Yangtze ridge, so that while the former yields pre-eminently a summer flora, the latter is typified by an autumn flora; I have found gentians in bloom on the Yangtze ridge in October at 16,000 feet, when at the same time deep snow extended from 12,000 feet on the Salween side.

As to the ridges west of the Salween, I may mention that in A-tun-tsi I met an official who two years previously had crossed from the Salween to the 'Nmai-kha and beyond, somewhat to the north of Prince Henry's route, and another Chinaman who had accompanied Prince Henry himself in 1895. Both men spoke of dense jungle throughout the journey, of tigers and elephants, and of continuous drenching rain; but when I asked if it would not be possible to cross during the fine winter months, they thought that the snow on the passes would be too deep.

The main formations, then, owe their nature to the summer rains of the S.W. monsoon, but when we come to details in any particular locality, we find the effect of these conditions to a considerable extent masked by superimposed conditions directly due to the topographical peculiarities of the country, namely the trench-like valleys immediately overshadowed by the colossal peaks of the dividing ridges.

Throughout the vegetative season a strong wind blows through these funnels from the south, and, sweeping up the side ravines which gash the dividing ridges, spreads out, becoming less regular and less violent, though still maintaining its character, that of a warm dry wind carrying little moisture ; so that on the high plateaux of the Yangtze-Mekong divide to which the following remarks principally refer, I have noticed this desiccating south wind blowing chiefly during the mornings.

The effect of such a prevailing wind is very clearly marked in the case of valleys and slopes facing south, and therefore freely exposed to it, though this effect is considerably more marked in the case of the latter, for reasons which will appear later (Pl. 7, Fig. 2).

Before comparing ridge with ridge and valley with valley, however, it will be convenient to consider the complete sequence of formations on the Yangtze-Mekong divide, where five well-marked belts may be distinguished, as follows :—

(1.) The forest-belt with *Abies, Quercus, Rhododendron,* and deciduous-leaved trees such as *Larix, Betula, Acer, Pyrus,* with other familiar north temperate genera : (2) the shrub-belt with *Rhododendron, Rosa, Potentilla, Cotoneaster, Berberis* and *Salix* conspicuous : (3) the belt of dwarf Rhododendrons ; and finally the alpine grassland belt (4) marked by a wealth of Primulas, Saxifrages, Gentians and many other plants, gradually giving place to (5) an open scree-formation, of which more anon (see Section, p. 338).

The limiting altitudes of these belts cannot be set down with any degree of accuracy, and indeed the object of this paper is to point out how, and, if possible, why they vary within wide limits ; so much so that in one locality the tree-limit stands at about 14,000 feet and is succeeded by a well-developed shrub-formation, while in another locality it stands at over 15,000 feet and dwindles directly into alpine grassland, thus skipping two distinct formations which elsewhere are conspicuous enough.

The plateau valleys of the Yangtze-Mekong divide are of course exposed to the desiccating winds from both main valleys, but on their upper limits towards the water-parting it will often be found that one up-valley wind prevails, and thus becomes a down-valley wind on the other side.

Such a down-valley wind from the cold plateau is always a rain-bearing wind, and consequently these valleys present more or less the same characteristics as valleys facing directly north ; we may instance the valley, facing north-west, between A-tun-tsi, above

W.

E.

Thousands of feet
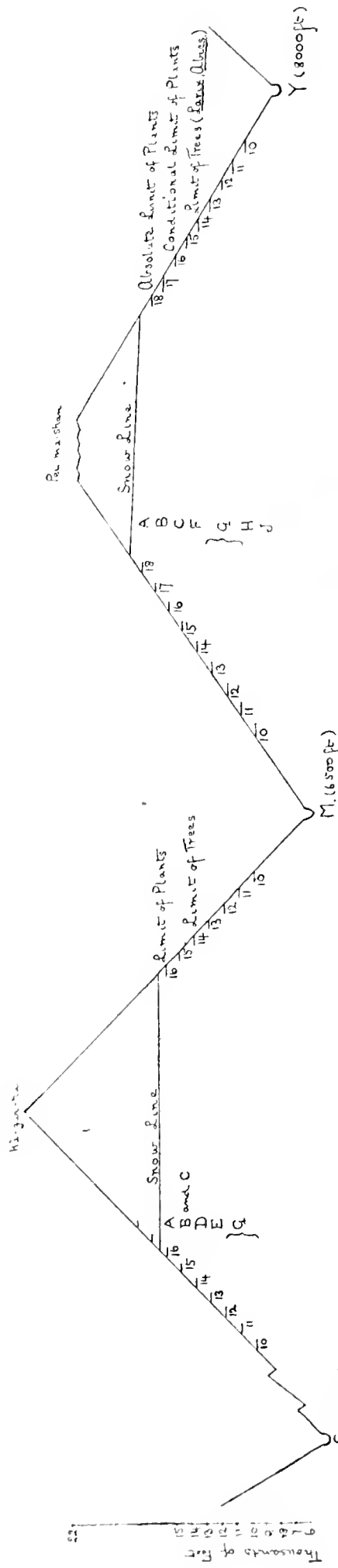
Diagrammatic transverse section from west to east (Salween river to Yangtze river) in 28° 15' N latitude to illustrate the sequence of vegetation on the descending ridges, with missing belts and blank limits.

Ha-gu-ra

Snow Line

Limit of Plants

Limit of Trees

Snow Line

B and C
A
E
G

S. (5000 ft)

M. (6500 ft)

Pei-ma-shan

Absolute Limit of Plants

Conditional Limit of Plants

Limit of Trees (Poa alpina)

Snow Line

A
B
C
F
G
H
J

Y (8000 ft)

Miles

1 2 3 4 5   10   20

Vertical Interval : Horizontal Equivalent = 2.6 : 1

Mekong - Salween Watershed

16000 ft	A	Open scree formation
15000 "	B.C	Alpine grassland, dwarf Rhododendrons
14000 "	D	Alpine meadow
13000 "	E	Alpine forests of Alnus and Betula.
	F	Wanting
12000 }	G	Forest of Abies, Rhododendron,
11000 }		Cunninghamia and Deciduous Trees.
	H	Wanting
10000 "	J	Dry region. Pinus

Mekong - Yangtze Watershed

18000 ft	A	Open scree formation
17000 "	B	Alpine grassland.
16000 "	C	Belt of dwarf Rhododendrons
	{D	Wanting
	{E	Wanting
15000 "	F	Belt of Shrubs
14000 "	G	Forest of Abies, Rhododendrons
13000 "		and Deciduous Trees
12000 "	H	Belt of scrub oak
11000 "	J	Arid region. Pinus

the Mekong, and Pang-tsi-la by the Yangtze, which, swept by the wind from the high plateau, was drenched with rain day after day when bright sunshine (depending on the wind from the Mekong below) prevailed at A-tun-tsi, distant a few miles as the crow flies.

The most pronounced result of this is that the same flowers open one or two months earlier in the former valley than in the immediate vicinity of A-tun-tsi—an important point.

All south-facing valleys are directly exposed to the raking wind already mentioned, and under such conditions the tree-limit may be lowered by as much as a thousand or fifteen hundred feet. This is probably a direct result of desiccation, since from such valleys even the deciduous-leaved *Larix* is entirely absent; *Abies* and *Juniperus*, both pronounced xerophytes, being the limiting species, and these scarcely occurring above 14,000 feet.

Not only is the upper limit of trees thus curtailed, but the lower limit of the forest-belt is considerably raised. Thus in the A-tun-tsi valley, which is peculiarly exposed to the savage winds of the Mekong gorges, there is no forest at all below 11,000 feet, and deciduous-leaved trees are the exception, whereas in favoured valleys the forest-belt may begin below 10,000 feet, in which case there is usually a well-marked transition from deciduous-leaved trees in the valley-bottom *(Populus, Betula, Juglans, Acer)*, to *Quercus* and *Pinus* on the rocks and finally *Abies* (often with *Larix*) at the valley-head.

In the former case, as at A-tun-tsi, the place of the lower forest-belt is taken by another shrubby belt, composed chiefly of scrub-oak, but it may include, on limestone rocks, scattered pines, as above Pang-tsi-la.

On the road from A-tun-tsi to Batang the Tsa-lei-la is crossed at an altitude of 15,800 feet, this pass facing due north and south. On the A-tun-tsi or Mekong side, facing south, alpine grassland prevails for the last 1,500 feet, broken here and there in the shelter of the rocks, to within a few hundred feet of the summit, by patches of dwarf Juniper only; on the Batang (Yangtze) side facing north, forests of *Abies* and *Larix* extend to within six or seven hundred feet of the pass, finally giving place to a narrow belt of dwarf Rhododendron, which in favoured situations extends practically to the summit, though on the southern slope there is no Rhododendron within a thousand feet of the summit.

Yet the herbaceous alpine flora is but little affected—in the valleys alpine grassland is almost indifferent to the wide range of conditions—the shrub-flora is more affected, and the forest-belt most of all.

It seems probable that the absence of *Larix* from the south slopes is due to summer, not to winter conditions, for no deciduous-leaved trees extend to the limit of trees on that side, whereas deci-duous-leaved shrubs do; the limiting trees are in fact pronounced xerophytes protected against excessive transpiration. In north-facing valleys *Larix* usually shares with *Abies* the position of limiting species, and I have seen it, stunted and wind-torn, at well over 15,000 feet. But besides exposure to the prevailing wind, other abnormal conditions result from the southern aspect, namely the early melting of the snows, partly we may suppose owing to the warm south-west winds, and partly to these slopes being in full sunshine throughout the day. The low altitude of the sun during the early spring makes this last difference more pronounced in the case of the higher and steeper ridges.

The effect of this is twofold. In the first place a warm protective covering is rapidly stripped from the mountains, thus exposing the vegetation to a dry wind at the very commencement of the season, naturally the most momentous period in the life-history of the plant, since it finds itself for the first time thrown entirely on its own resources; in the second place, the only water-supply on which the vegetation can confidently depend till about the middle of June, when the rains break, is removed at the precise moment when it is most required (compare Pl. 7, Fig. 3, with Pl. 8, Fig. 1). -

In the second week of June we crossed the Mekong-Salween watershed at an altitude of 14,000 feet, the pass facing E.N.E. and W.S.W. (Pl. 8, Fig. 2). Ascending the eastern slope we trudged through deep snow for three hours : but at the summit the snow ceased abruptly in a high bank, and the western slope, which was extraordinarily precipitous, was clear of snow for nearly a thousand feet, though a big drift still lay on the gentler slope below. We crossed the same pass again in the second week of November, and were probably the last to get over, for the snow lay deep on both sides as low as 12,000 feet ; at the same time there was no snow on the Mekong-Yangtze divide below 15,000 feet. The three passes by which we crossed the Mekong-Salween divide, ranging from 13,000 to 15,000 feet, are quite clear of snow for possibly four months in the year, and are passable from June to November; on the other hand the Run-tsi-la, a pass from the Mekong to the Yangtze, which we crossed in mid-October, is over 17,000 feet and can be crossed from June to December, being clear of snow for about three months.

Incidentally two other points call for notice.

In the first place a snow-clad slope is to a large extent protected from atmospheric denudation, and, weathering being in excess of transport, it presents both a gentler grade and a more broken surface than does the exposed slope; this I think in itself affects the composition of the flora, permitting many plants to find shelter on the one side which is denied them on the other.

Secondly, while a high pass near the tree-limit is always bare of trees for some hundreds of feet, even on the sheltered side, yet scattered forest may extend up the valley sides wherever it can find foothold, to a height well above the actual col on the north face, though not on the south face, a phenomenon undoubtedly due to the fact that a well-marked col is raked by a sharp up-valley wind on *both* sides, as I have observed on several occasions.

In July, seeing that the vegetation on either side of a north and south facing pass at an altitude of about 16,000 feet was very similar near the summit of the pass, but exhibited distinct formations to north and south a few hundred feet below, namely alpine grass-land in the former case, and scree vegetation in the latter, I took the soil-temperatures, an up-valley wind blowing from either direction.

On the north side, thirty yards from a large patch of melting snow the soil-temperature was 52·7°F., the air-temperature on the ground 47·5° F, and in the wind five feet above the ground 43·7°F.

On the south side the same positions gave precisely the same readings, showing the similarity of conditions, as regards temperatures which vitally affect the functioning of a plant's organs, on either slope near the summit of a high pass. (The wind-temperatures here noted may of course be neglected so far as the existing vegetation is concerned, since at that altitude no plant rises more than a few inches above the ground, largely for that very reason however).

This similarity of vegetation does not apply in the case of a *ridge* exposing north and south slopes, for the summit of the ridge marks the division between dense scrub vegetation and bare scree.

On the south side of such a ridge, on July 19th, at an altitude of 15,000 feet, I obtained 56·3° and 49·5°F. for soil and air respectively, while on the north side I got 59·9° and 58·1°F. within a stone's throw of the former readings. It is evident then that a col exercises considerable local influence on the formation.

Exactly the same principle is illustrated in the case of valleys

which extend to well beyond the limit of trees. In this case the trees end sooner in the valley-bottom than they do on the enclosing mountain slopes, due to the concentration of the wind along the valley-bottom as the mountains rise higher, since the enclosing ridges usually rise more rapidly than does the floor of the valley (Pl. 7, Fig. 3.) The shrub vegetation on the other hand, usually represented at these altitudes by dwarf *Salix*, extends further up the valley-bottom than it does up the mountain slopes (where the place of *Salix* is taken by Rhododendron), for the reason that the water-supply concentrates in the valley-bottom.

Wind and water are indeed the two continuously warring factors which determine the formation and its limit, the selection of a certain type of vegetation being dependent on its invulnerability to the ravages of one or lack of the other: when at last they combine forces they quickly overwhelm *all* forms of vegetation.

To sum up, the tree-limit varies between approximately 14,000 and 15,500 feet, with local peculiarities of distribution dependent on topographical details; it is determined by the level at which absorption of water, more and more retarded by removal of the protecting snow-blanket and consequent lowering of the soil-temperature, is finally overbalanced by the rate of transpiration, more and more accelerated by a prevailing wind.

In north-facing valleys pre-eminently, the forest-belt, which here begins with deciduous-leaved trees and includes *Larix*, up to the limit of trees, passes rather abruptly into a scarcely developed belt of dwarf Rhododendron immediately giving place to alpine grassland; in south-facing valleys, the forest-belt, which towards the tree-limit comprises only evergreen Conifers, passes gradually into a well-marked shrub vegetation, which in turn gives place to dwarf Rhododendron and alpine grassland.

Valleys facing in intermediate directions are dependent for their characteristic vegetation not so much on the presence or absence of the prevailing wind as on the fact of its blowing up or down the valley, a circumstance varying with the topographical features of the surrounding country.

While valleys well exhibit the effects of wind and water both in the composition of their flora and in the different altitudes at which a particular formation is curtailed, such differences are, as already indicated, still more clearly marked in the case of mountain ridges; and here the problem is simplified by the appearance of an entirely new formation, namely desert.

In the middle of May, at an altitude of 16,000 feet, we found a south-facing slope, consisting of scree material, dry on the surface and clear of snow, where one had to look carefully to find scattered plants—a *Ranunculus*, one or two Cruciferæ and Umbelliferæ, a *Corydalis*, a "cushion-plant" belonging to the Caryophyllaceæ, and a few others (Pl. 7, Fig. 1).

Crossing the crest of the ridge and attaining the north slope we immediately found quite a different state of affairs.

Here a thick carpet of dwarf shrubs, chiefly Rhododendron and *Cassiope*, with a shrubby saxifrage, grew in a comparatively rich loamy soil, and large patches of melting snow still remained, the water from which kept the entire slope moist. The transition was abrupt, the contrast extraordinary. A bitterly cold wind came slashing up the screes from the south, but immediately below the crest of the ridge, which was only a few feet wide, protection was guaranteed to the vegetation and genial warmth prevailed.

The bare screes commenced at an altitude of about 15,500 feet, almost immediately succeeding the limit of trees in the lower part of the valley, and the limit of shrubs in the upper part; they extended another thousand feet higher, to the peak dominating the valley-head.

Looked at from a little distance, the limit of plants on such a south-facing slope is practically a straight line, the belt of dwarf shrubs ending abruptly on the screes at an average altitude of 16,000 feet. This I call the Conditional Limit of Plants, and it may be defined as the altitude at which the rate of transpiration due to full exposure to the south wind is equal to the rate of absorption by the roots from an increasingly drier soil.

It will be noted that this limit is always marked by a belt of dwarf shrub vegetation, and that it is the alpine grassland belt which is lacking. True, careful search will, as indicated, reveal scattered scree-plants above the assigned limit, but the chief point is that the complete sequence of belts is interfered with, the dwarf shrub belt being immediately succeeded by desert, the scattered vegetation of which is highly specialised to meet the changed conditions.

In October, as previously stated, we crossed the Rün-tsi-la, a pass between the Mekong and the Yangtze, not much less than 18,000 feet above sea-level, and the ferocious wind which bit through everything was alone sufficient to blast all vegetation from the ridge at that altitude.

Though the pass was of course under deep snow, the limit of plants was evidently some hundreds of feet lower down, and to shew how little mere surface cold affects plant life during the brief vegetative season, it may be remarked that two species of gentian were blooming in the snow. The importance of water too was illustrated by the manner in which the final concentration of the vegetation at the plant limit occurred where the trickles of water came from the piled screes, an aquatic *Senecio* being indeed one of the last survivors.

The fact that the vegetation at this altitude is clear of snow for or two or three months only, seems no hindrance to it, while the autumn gentians must perforce flower actually in the snow.

If we now turn our attention to the protected slopes and gullies of a mountain mass rising above the snow line, we find a different state of affairs. Above 16,000 feet the dwarf Rhododendron belt gives place to alpine grassland, which, so long as it is completely protected (that is by facing north), remains practically a closed formation till an altitude of about 17,000 feet is attained, after which screes, consisting of big angular blocks of stone, meet the eye on every hand. On south-facing slopes these screes are absolutely devoid of plant life, but wherever protection is guaranteed by ridge or rock-face, a very considerable open formation maintains its existence for, so far as I was able to ascertain, another thousand feet, and this must in no wise be confounded with the totally different flora of the exposed screes to which I have just alluded.

This open formation consists of semi-aquatic plants growing in rock-pools derived from melting snow, " cushion-plants," and terrestrial herbs presenting no obvious specialisation, and even at an altitude of approximately 17,500 feet comprising a considerable variety, of which the most conspicuous are *Primula, Allium, Scirpus, Meconopsis, Saxifraga, Sedum, Potentilla, Aconitum,* and two species of Caryophyllaceæ (" cushion-plants ") with a few aquatic species.

At mid-day on July 23rd (altitude 17,000 feet approximately) I took the temperature of the water in one of the streams derived from the snow above, and at different points obtained temperatures of 37·4⁰F. and 37·2⁰F., a Crucifer being at this time actually in the act of ripening its fruits under water.

In September, I climbed higher, attaining an altitude of nearly 18,000 feet, still finding *Meconopsis* and " cushion-plants " in shaded crevices ; a severe snow-storm prevented my reaching the very last flowering plants on this occasion, but we may regard 18,000 feet as

the limit, and this I call the Absolute Limit of Plants. It is important, I think, to distinguish between these two limits, as the following consideration will shew.

It is as easy for a plant to obtain protection from the wind at 19,000 feet as it is at 16,000 feet, so that evidently a new factor comes into play and determines the absolute limit; this I take to be the decreasing temperature of the soil, which, as the snow-line is approached, entirely checks absorption by the roots. The Absolute Limit of Plants then, may be defined as the altitude at which the rate of absorption by the roots from an increasingly colder but nevertheless moist soil, is balanced by the rate of normal transpiration at this altitude.

On the Mekong-Salween divide the greater rainfall and consequent lowering of the snow-line makes the conditional limit of plants coincident with the absolute limit, since now the controlling factor of the one, namely, an abnormal rate of transpiration due to wind action, becomes effective at about the same altitude as the controlling factor of the other, namely, an abnormal decrease in the rate of absorption due to the coldness of the soil. Hence the distinction cannot here be maintained; in fact, the distinction itself is characteristic of highly abnormal conditions.

That the mere fall of temperature alone is not responsible for the final cessation of plant-life, is suggested by the results obtained when taking the temperatures of certain " cushion-plants."

Plunging the bulb of the thermometer into different species of " cushion-plants " I obtained the following readings:—59°, 64·4° (twice), 59·9°(twice), 52·8°F., the corresponding soil temperatures being 53·6°, 60·35°, 52·7°, 54·5° (twice), 49·1°. The " cushion-plant " thus maintains an average temperature 6·98°F. in excess of the average soil temperature; so that simply by assuming the "cushion" habit a plant is able both to reduce transpiration to a minimum and to keep up its own temperature.

One further point calls for consideration, but can only be touched on here, since it opens up a wide field for investigation.

There is good reason for believing that the Yangtze-Mekong divide was, in times geologically recent, seamed with glaciers reaching down to about 14,000 feet; and, granting their former existence, their disappearance is more likely due to an amelioration of climate or a change in the seasonal distribution of rainfall than to a general depression of the ridge, since we should have to postulate an average lowering of several thousand feet.

Pei-ma-shan (see map, p. 334), a mountain on the crest of the watershed rising some thousands of feet above the snow-line to the S.E. of A-tun-tsi, possesses several glaciers which are clearly retreating; their bottle-nosed snouts, their lateral moraines extending for some distance beyond the present limit of the ice, and the isolation of their terminal moraines, leave no doubt on the point.

Other evidence is afforded by small mountain lakes which constantly occur between 16,000 and 18,000 feet, occupying depressions in the screes, or rock-basins, sometimes of great depth ; by the fact that many of the valleys immediately descending from the watershed are " hanging " valleys, and present further a peculiar step-like or " tread and riser " ascent at their upper extremities; and finally by the immense piles of angular scree material, bearing a strong resemblance to morainic material, which occupy the valley heads ; indeed, the scree shewn in the photograph (Pl. 7, Fig. 7) might well be a lateral moraine. If this is actually the case, the flora is an *ascending* one, and it is to the circumstance that new ground has probably for long periods been gradually opened up for colonisation that I attribute the large number of species of certain successful genera, such as *Saxifraga* and *Gentiana*, found towards the limit of plants in N.W. Yunnan ; it seems to indicate a *changing* climate on that curious geological freak, the Mekong-Yangtze watershed.

DESCRIPTION OF PLATES VII AND VIII, ILLUSTRATING MR. F. KINGDON
WARD'S PAPER " ON THE ALTITUDINAL LIMITS OF PLANTS IN
NORTH-WEST YUNNAN."

PLATE VII.

Fig. 1.   Mekong-Yangtze watershed, screes at 16,000 feet.   These screes face south and are clear of snow in the middle of May.   The dark patches are Juniper and dwarf *Rhododendron*.   Just over the ridge on the extreme left (not shown) and facing north, is a thick carpet of undershrubs with patches of melting snow.

Fig. 2.   Mekong valley, arid region at 7,000—8,000 feet.   Cultivation is only possible where a mountain torrent offers facilities for irrigation.   Barley on the terraces, with walnut trees.   In the foreground *Selaginella involvens*.

Fig. 3.   South-facing slope at 15,000 feet showing scrub-oak and bare scree.   Higher up the limit of *Abies* is seen.   It has been driven out of the valley by the concentration of the winds at high altitudes, and obtains protection just over the ridge.

PLATE VIII.

Fig. 1.   Taken from the same point as the Plate VII, Fig. 3, but looking the other way.   North-facing slope showing *Rhododendron* in place of scrub-oak, and no screes.   *Abies* at the Limit of Trees, here able to withstand conditions in the valley-bottom, giving place to shrub-belt.

Fig. 2.   Mekong-Salween watershed below the Sie-la, 13,000 feet.   Alpine meadow in the foreground.   Higher up is *Abies*, which cannot survive in the valley-bottoms near the passes, owing to concentration of wind.

EXPERIMENTS ON THE ORIGIN OF SPECIES IN THE GENUS *HIERACIUM* (APOGAMY AND HYBRIDISM)[1].

By C. H. Ostenfeld (Copenhagen).

I.

AS is well known, *Hieracium* is a very polymorphous genus. Specialists have been able to distinguish numerous minor species ("petites espèces") or separable forms which nevertheless stand so near to each other that a botanist not familiar with the genus hardly distinguishes one from another. In Scandinavia for instance Dr. Dahlstedt and his pupils have distinguished many hundreds of such species in the sub-genus *Archieracium* alone, and in the British Isles the number of minor species is also fairly large.

During several years (since 1903) I have studied this interesting genus in order to find out the causes of this polymorphy, or at least to trace facts which stand in relation to it, and I think that I have found such facts in the apogamy and hybridism which occur in the genus.

In 1903 Raunkiær and I proved that many species are apogamous, *i.e.*, that they produce fertile seeds without fertilisation. Earlier than that Raunkiær had shown that the species of *Taraxacum* are apogamous. His method is very simple : he cuts off with a razor the upper part of unopened flower-heads, thus removing both the anthers and the stigmas; heads treated in this way—"castrated"—grow out and give fertile seeds, obviously without any fertilisation. The same method has been applied by us to the *Hieracia* and with the same effect, as regards many, but not all species.

It was thus shown that many *Hieracia* are apogamous, but no information was found relating to the details of the apogamy. Cytological studies by S. Murbeck and O. Rosenberg have cleared the matter up. I shall not enter into details on this point, which may be found in the papers published by these authors; it will be sufficient to say that, in some cases, the mother-cell of the embryo-sac grows out to form an apogamous embryo-sac, whilst in other cases a cell from the nucellus is transformed into an apogamous embryo-sac. In both cases this embryo sac has the

[1] Read before the Botanical Section of the "British Association" at Dundee, September, 1912.

unreduced number of chromosomes. Therefore I speak of apogamy, not of parthenogenesis.

II.

The genus *Hieracium* has been divided into three sub-genera, which are widely separated from each other, and which also differ as regards their apogamy.

One sub-genus, *Stenotheca*, is rather small; it has only one species in Europe, *H. staticifolium* of the Alps, and several species in America. I have had two American species and the European one in culture, and have found that none of these three species gives fruit after castration. One of the American species has been studied from a cytological point of view by Rosenberg and was found quite normal. Thus the sub-genus *Stenotheca*, as far as it has yet been investigated, is quite normal and requires fertilisation for producing seeds. As far as I know, no polymorphy is found in it; and on the whole, in contrast to Europe, polymorphy in *Hieracium* has not been recorded from America.

The second sub-genus *Archieracium*, on the other hand, is very polymorphous; the greater number of the many minor species thus far described belong to it. Its species are very numerous in Europe; some occur also in Asia, and a few in America. Very probably, in Europe, new forms of this sub-genus are appearing at the present time, and it is an interesting fact that many of the described species have an extremely limited distribution, which points to a very recent origin.

I have made experiments with many (about 65) species or forms of this sub-genus and have found that nearly all are apogamous, and by counting the numbers of fertile seeds in castrated and in non-castrated heads, I think I have shown that nearly all species examined are absolutely apogamous, *i.e.*, no flower is capable of fertilisation. Only two species, namely *H. umbellatum* (which is rather a group of species) and *H. virga-aurea*, require fertilisation for developing fertile seeds, giving no seeds after castration. Nevertheless I have had one form of *H. umbellatum* which is apogamous, and in this case the number of fertile seeds in the castrated heads was not so large as the number in non-castrated heads. This means, probably, that some, but not all, of the flowers of a head are apogamous, some requiring fertilisation. A few other species are likewise only partly apogamous, judging from the comparative number of fertile seeds in castrated and non-castrated heads. Thus we have three stages in the development of apogamy :

1. Species which require fertilisation, *i.e.*, sexual species;

2. Species which are partly apogamous;

3. Absolutely apogamous species.

Lately I have examined the pollen of a number of species and have found some interesting points with regard to its development. I have to premise that no observer has yet succeeded in obtaining germination of the pollen of Compositæ in artificial cultures (Molisch, Lidforss), nor have I myself succeeded. Therefore, when testing the germinative power of the pollen we can only observe whether any grains have germinated on the stigmas, or whether when laid in water or a solution of sugar, they throw off the exine at the points where the pollen-tubes should protrude. I have mostly used the latter method of investigation and have found that the few sexual species examined, *H. venosum* and *H. staticifolium* of the *Stenotheca*-subgenus, and *H. umbellatum* among the *Archieracia*, have quite normal pollen, all the grains being about equal in size, and in water showing the exine thrown off at the points indicated. Among the apogamous *Archieracia* some species have pollen which has degenerated into a few yellow-brownish lumps, and in these species the anthers look empty; hence these species are functionally female. In other species we find pollen consisting of grains very unequal in size, a greater or smaller number of them very small and evidently not fertile, while the rest are of the normal size and look fertile ; but they do not throw off the exine when laid in water, and I suppose that this pollen also is incapable of germination. Thus in the apogamous species where there is no use for the pollen, it is degenerate. Another question which I cannot answer, is whether or not the degeneration of the pollen preceded or has followed the acquisition of apogamy.

The third and last sub-genus, *Pilosella*, stands between the two others as far as apogamy is concerned. Most of the species are apogamous, a few are sexual, but the apogamous ones are not absolutely apogamous, a fact that appears from the number of fertile seeds in castrated heads and from the power of hybridizing in many species. As far as my investigations go, the pollen is usually fertile, but I have not yet examined many species ; and in some it has degenerated to brownish lumps or is wholly wanting. I have not found the intermediate stage which is so common in *Archieracia*, the *Pilosella*-species being either wholly hermaphrodite or purely female.

III.

Having reviewed the sexual conditions in *Hieracium*, we may now turn to the question of the origin of new forms. These must arise either (i.) by hereditary variations of already existing species, or (ii.) by crossing between them, or (iii.) by a combination of both these methods. My experiments show that new forms arise by hybridisation and seem also to allow the first possibility. Thus in *Hieracium* new species arise both by hybridisation and by hereditary (single) variations (so-called mutations), and the continued existence of the new forms is favored by prevailing apogamy which prevents the blending and ultimate effacing of new characters through repeated crossings back with the parents.

Hitherto my hybridisation experiments concern only species of the *Pilosella*-sub-genus. The few exact experiments with *Archieracia* have not yet given positive results. But Mendel made two actual crosses with *Archieracia*, both having *H. umbellatum* (which we now know is sexual) as the one parent; and a plant of *H. virga aurea* (also a sexual species) in my cultures gave without isolation a heterogeneous offspring with hybrid-looking individuals.

Mendel also made many hybridisation experiments with *Pilosella*-species, and I can confirm his results. The most salient matter is that the first generation, F_1, is heterogeneous, in contrast to the ordinary rule for hybrids. The following generations, F_2, F_3, etc., are homogeneous and like their individual parent in F_1. In other words, the *Hieracium* hybrids behave in just the opposite way from other hybrids, in which F_1 is homogeneous, whilst the later generations segregate. The explanation of the non-segregation is to be found in apogamy. As was said above, the *Pilosella* species are only partly apogamous and it is possible to cross two such species with each other. We get then an offspring which consists of (i.) some individuals like the mother and of (ii.) some individuals which are evidently hybrids, but each of which differs from the others. The individuals which have the appearance of the mother have, probably, been produced apogamously, while the others are the result of crossing. The hybrids obtained are often wholly or nearly sterile, and thus segregation in the later generations cannot, by the nature of the case, be observed. However some of the hybrids are partially or wholly fertile and these are apogamous, as are one or both parents; and consequently the later generations remain like their offspring of F_1. In other words, by means of

crossing new forms do actually arise; and they are at once perfectly constant, and behave like ordinary species. My experiments have at present reached the fifth generation and in several cases I have had more than 100 individuals of a single generation, all the plants of which were alike, and like the F_1-individual from which they were derived. I have commonly used the orange-red *H. aurantiacum* as male parent, because it is so easy to trace its influence in the colour of the corolla of the hybrids. The following figures will show the extent of some experiments:—

Number of individuals of the different generations of two crosses between two *H. excellens* and *H. aurantiacum.*

	F_1	F_2	F_3	F_4	F_5
No. 46₁	1	3	12	—	—
No. 46₂	1	110	38	—	—
No. 46₃	1	52	3	28	—
No. 46₄	1	38	205	17	14
No. 48a	1	14	106	30	16

Sister hybrids from the same cross.

In all my experiments the rule of constancy of the later hybrid generations has held good with one exception: in the F_2 of No. 46₃ there appeared one very aberrant individual—a mutant—which unfortunately was sterile and the behaviour of which by isolation and by crossing consequently could not be investigated.

As an example of the heterogeneity of the F_1-generation I may mention that a single cross between *H. auricula* (a sexual species) and *H. aurantiacum* gave twenty-nine hybrid-individuals all of which differed from each other. Most of them were sterile and weak and have since died, but a few of them proved to be fertile and at present have reached the third generation. The individuals of the F_2 and F_3 generations remain like the individual of the F_1 generation from which they sprang.

It is thus evident that hybridisation plays a rôle as a factor in the origin of new forms in the sub-genus *Pilosella*, and it is probable that many forms have originated in this way. On the other hand,

the origin of new forms in the sub-genus *Archieracium* must go on otherwise, at least in the absolutely apogamous forms. A Swedish botanist, Samuelsson, has shown that some forms have a very limited distribution and that their areas fall within the area of nearly related, more widely distributed forms, and further that they seem to have a centre from which the distribution extends, all the evidence pointing to this centre as the place where the form in question has arisen. Presuming that his forms also are apogamous, the forms of restricted distribution must have arisen by means of a variation which because of apogamy is at once fixed, since it cannot be mixed by crossing with the original form. If this supposition is correct, it should be possible always to obtain new forms by cultivating a sufficient number of individuals of a species, and, probably, it would be best if the species chosen for such an experiment were a form of wide distribution, *i.e.*, a comparatively old form. Working on this hypothesis I have cultivated rather large numbers of individuals—as large as the space at my disposal would permit—of certain forms, and have always used those whose constancy I had tested beforehand by castration and by sowing the seeds. Also the seeds for the experiment were obtained from heads which had been castrated ; thus no kind of fertilisation had taken place. The number of individuals obtained reached between 100 and 300 in each experiment, and while three experiments did not show any variation, the fourth one with a form of *H. tridentatum* from Denmark gave the result that 152 individuals were alike and like the parent, but one individual differed in several respects with regard to the involucral bracts, the length and direction of the corollas, etc. This variant was castrated, and the seeds obtained from it were sown. The seeds have germinated ; but only a few of the plants have yet flowered. Thus I do not know what the whole offspring will prove to be ; but the few flowering individuals look exactly like their parent, keeping its distinctive marks.

The material for showing the origin of new forms by means of variations is consequently somewhat meagre at present ; but to the experiment just described and to the facts put forward by Samuelsson must be added the above mentioned variation of a cross in the F_2-generation. Further a single variation found in a culture of *H. aurantiacum* originated as a cross between two different races of this species : 167 individuals were all alike and like the mother, but one differed from the others and did not show any character of the " father," which undoubtedly has no influence. The distinctive

marks of this individual were so expressed that its appearance was quite unlike that of either parent.

If we take all these facts and arguments together, it is, I think, permissible to say that new forms may arise by means of single variations, *i.e.*, mutations, which may be classed under bud-mutations, as no fertilisation is required for their appearance.

My position may be summarized in a few words, as follows : *in Hieracium new forms arise by means of hybridisation and also by means of single variations ; in both cases the prevailing apogamy supports their existence and constancy ;* thus polymorphism in the genus is correlated with apogamy, but it is not allowable to draw any conclusion as to causality between them.

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THE INTERNATIONAL PHYTOGEOGRAPHICAL

EXCURSION IN THE BRITISH ISLES.

X.—Additional Floristic Notes.

By G. Claridge Druce.

(Oxford).

IN the preceding chapters devoted to this subject, which have appeared in the New Phytologist, our foreign *eonfrères* have dealt with the salient features of our delightful excursion in a most interesting manner. In one of them (p. 55, 1912) Dr. Rübel, in his suggestive note on the Killarney vegetation, names the Violet we gathered there as *V. silvestris* var. *pseudo- mirabilis*, while Dr. Ostenfeld (p. 114) in a masterly manner gives details of some of the critical forms noticed on the expedition, and names some new forms for Britain. Dr. Graebner (p. 170) in his valuable paper mentions *inter alia* some of the plants which have become naturalised in Britain, while Professor Drude (p. 236) in his erudite and thoughtful " Comparison of the Flora of Great Britain with that of Central

Europe " gives us many themes for thought, not only from an
ecological but from a systematic standpoint.

My own notes (pp. 306—328, 1911) were published so soon after
the excursion, that in some cases the names given were only provi-
sional, and many more had to be submitted to the fire of criticism,
but in no case was any dogmatic statement made. One is too
conversant with the variability of nature, and too cognisant of one's
own imperfect knowledge to give hard and fast definitions or to
refuse to recognise that a plant may be looked at from more than
one point of view—the characters on which one authority relies for
definition are not always those which another chooses—so that when
one is dealing with some of the plastic species, it is quite evident
that discordant opinions may result. It is sufficiently obvious that
a number of botanists drawn from a wide area in Europe would
have different systems of nomenclature, and would take divergent
views as to the limitations of species and the lower grades into
which plants have been divided. Yet on the whole it was rather the
general agreement, than the instances of difference which impressed
me. One fact, however, stood out as a prominent feature, namely
that whereas many leading British systematists have been extremely
reluctant to acknowledge that the British Isles contained endemic
species—for instance Sir J. D. Hooker in the preface to Wallace's
Island Life, where the suggested endemic species were almost
entirely rejected, either as not being endemic or as not being species.
Yet, as one would expect, a more minute and critical study of plant
forms, especially by observers working in the field, rather than in
herbaria— since in the latter one only sees a specimen or two and
not the group, sees it only in part and not as a living entity, so that
the field student is able to notice many points of difference, some
so minute as to elude our power to adequately define, and yet
other variations which can not only be seen but described—has led to
well-marked differences being established between many of our
island species and their homologues on the mainland of Europe.
Drude (l.c. 237) well says "very many common species constantly
polymorphic in their German stations appear to me to look very
different in England, to represent in fact slightly differentiated
examples of local endemism. How otherwise can we interpret the
Birches for instance ? .... I may say that I gained the impression
of numerous slightly differentiated local forms, endemic in England."
For an example of this local endemism attention may be directed
to so well known a plant as our Golden Stonecrop, which in Britain

we have called *Sedum acre.* Our Swiss and German *confrères* felt certain when they saw it growing in Lancashire, Westmoreland and Galway that it was not identical with the Continental *acre.* My friend Professor Graebner took it home and has grown it side by side in the Berlin garden with the German *acre,* and finds it differs in all its points. He writes " *Sedum Drucei* (ined.) belongs to quite a large number of forms endemic in Britain which last year were observed, . . . and which took quite the foremost place of interest. This group proves beyond a doubt that the flora of the British Isles in con- sequence of the early separation from the Continent possesses a far larger geographical individuality, and has received a less disturbed development than is found in the floras of other parts of Northern Europe." This statement is borne out by one's own experience ; one sees that the common species of Jersey have a different facies from those of our Midlands, while those of the north Scottish coast possess a distinct individuality from those of Devon or Kent. But it is only exceptionally that *specific* distinctions can be found. This range of variation, differing necessarily in degree, however suggests that we may be unwise when working with critical forms to attempt to identify the micro-species of *Geranium, Erodium,* the *Melanium* Violas and the critical species of *Rosæ, Euphrasiæ, Hieracia,* and *Taraxaci,* with continental names. In many cases I strongly suspect that the British plants are sufficiently distinct to warrant them being described and named. Indeed, as will be seen, two of our British plants, *Erigeron alpinus* and *Melampyrum pratense,* should bear, Dr. Ostenfeld suggests, other names. And if evolution be a fact, we might be prepared to expect these plants, living for so long under different climatal conditions and geographical position, should have evolved a facies of their own.

With the editor's kind permission I purpose giving a short resumé of some additional facts which have been obtained since the publication of my paper, to correct a few errors, and to avail myself of the opportunity of thanking my foreign *confrères* for their very great kindness and assistance in answering many questions, and for the manner in which they received the avowedly imperfect paper which dealt with the botanical gatherings made during that memorable excursion.

The number prefixed to the species is that given in my *List of British Plants.* When a species or variety is put in heavy type, it means either that it is new to the British flora or that the name is new. An asterisk (*) before a name means that the plant is alien. The sign ✗ means a hybrid.

20. *Ranunculus acris* L. On Crossfell a Buttercup occurred which I think must be referred to *R. acris* var. *Nathorstii* (Berl.), Druce, Ann. Scot. Nat. Hist. (1900) 166. I think it is the same as the large flowered Ben Lawers plant, gathered by me in 1897, and which Herr Freyn named *R. Nathorstii* A. Berlin in Öfvers. af K. vet.-Akad. Forhandl, (1884), N.7, pp. 20-21, a reference which I have been unable to verify. Dr. Graebner has grown it at Berlin, and finds it keeps its characters. It is the first record for England. But, as Freyn says, our *Nathorstii* does not exactly agree with the East Greenland plant, for the shape of the leaves is not quite the same. The carpels have a long beak.

48. *Caltha palustris* L. The small creeping form of this plant, which is the var. *minor* DC. of my *List*, was gathered by Dr. Graebner on Crossfell, and this also retains its character in culture and keeps quite distinct he says from *C. radicans* Forst.

77c. *Castalia alba* var. *occidentalis* Ostenf. in NEW PHYT., p. 116, 1912, under *Nymphæa* vel *Castalia*. By this name Dr. Ostenfeld now describes the plant which he showed us in Perthshire and then thought to be *Nymphæa candida* (NEW PHYT. (1911), 307) as also the plants gathered in Co. Galway. They would have been passed by me for *C. alba* var. *minor* (DC.), but Dr. Ostenfeld shewed us certain characters which separated them, he thought, from *alba* and induced him to name them *candida*. But as I pointed out (p. 308), *candida*, which I only knew from description, is itself a very critical and variable plant and in some parts of Germany where *C. alba* and *candida* grow together the two forms are with difficulty separated. Even in Dr. Ostenfeld's figure of our British plant the section of the ovary appears to be nearer to *candida* than to *alba*. I may also say that after I wrote my paper, on examining the pollen of our plants under a $\frac{1}{4}$-inch objective with that of *candida* with which I had been supplied, I found that it did not agree. We may therefore accept Dr. Ostenfeld's identification as being probably correct. Whether it is distinct from *minor* DC. has yet to be shewn, but it is quite likely a different form, and, perhaps, as Dr. Ostenfeld suggests, a plant of " acid-humus " habitats, whereas *alba* is found in more basic water. I saw it this year near Llanberis in Carnarvonshire, and although I was not able to gather it, almost certainly the same form was on the Moor of Rannoch.

In the *Flora of Hampshire*, p. 19, 1904, there is a reference to *Nymphæa alba minor* as occurring in 1739 : "in these pools I observed to grow (between Lyndhurst and Brockenhurst) both the small and great Water Lily; they were in blossom together, so that the distinction was easily made, and the difference was pretty remarkable," and I have noticed the same form in Virginia Water, Surrey and Berks. It will be interesting to see if these are distinct from Dr. Ostenfeld's variety. We may add that Caspary, an acknowledged authority on Water Lilies, treated *candida* as a variety of *N. alba*, and many authors consider it only a sub-species.

294. *Viola Riviniana* Reichb. var. **pseudomirabilis** (Coste) Gregory. This is the plant described by Dr. Rübel (p. 55) as *V. silvestris* var. *pseudomirabilis*, but more correctly placed as above by Mrs. Gregory in her *British Violets* (1912) under the above species. Coste (Bull. Soc. Bot. Fr.XL. (1893), p. CXV described it as a species while Becker (*Mon. Violae*, p. 12, 1910) treats it as a hybrid of

Viola mirabilis and *V. Riviniana*, the former species not yet recorded from the British Isles.

327. *Gypsophila porrigens* Boiss. Alien with other Eastern species Galway bay, kindly named for me at Kew.

403 (2). **Sagina scotica** Druce in Rep. of Bot. Exch. Club (1911) 14 April, 1912. This is the Ben Lawers plant which in my paper (p. 310) I named *S. glabra* Fenzl. var. *scotica*; but even before the paper was printed I had seen that it could not be put under that species, since the Tirolean specimens with which I had compared it were, I found, not authentic. The petals of *S. glabra* are much longer than ours, besides other marks of distinction. This was borne out by specimens of true *glabra* kindly sent me by Prof. Schroeter. Dr. Ostenfeld identifies it as *Sagina procumbens* × *saginoides*=*S. media* Brügg (but with a wrong synonym—it should read *S. glabra* var. *scotica* Druce, not *S. glabra* Druce). This was his view at the time, and although strongly controverted by one or two of our *confrères* has some probabilities in its favour, though I think he places too much stress on the supposed barren condition of the plants. But its great abundance over considerable areas, its different flowering time, and to me the absence of evidence of the presence of *saginoides* in it led me to adopt Prof. Graebner's view that it was a distinct plant, which I have named *scotica* in the work cited above. Since doing so Prof. Graebner writes (July 8th, 1912) " the *Sagina* from Ben Lawers grows very well, it has flowers and well developed *ripe fruit*. It is right to take it as a *species;* it is very characteristic and cannot be a hybrid," and on August 21st " it is impossible that *S. scotica* is a hybrid! we cultivate it with *saxatilis* (*saginoides*), but I cannot find anything of this plant in *S. scotica*. It is without doubt near *procumbens*, but a quite different plant. It has had good fruits." In culture I find that it produces good seed, and although reverting in appearance towards *procumbens*, still I think keeps distinct. In my paper I suggested that it would prove to be often named *saginoides* (or by one of its synonyms) in herbaria, and I find quite a considerable portion of Scottish *saginoides* to be really *scotica*. It exists under that name in Babington's Herbarium. The acute botanist, Mr. Webb, had also in *Herb. Edin.* first labelled specimens of it *S. saxatilis* and subsequently thought it to be *S. procumbens*, while there are other specimens under *saginoides* on various sheets. *S. scotica* is not confined to Ben Lawers, for I have seen it from Craig Chailleach in Mid Perth; from Glen Callater, S. Aberdeen, and from Clova, Forfar; a distribution itself somewhat antagonistic to its being of hybrid origin.

488. *Geranium Robertianum* L. var. *Villarsianum* (Jord). Dr. Ostenfeld (pp. 118-119) believes the forms he collected in the west of Ireland cannot belong to this name. But while it is quite possible that he is correct, it is by no means certain whether we are speaking of the same gathering, since I had three distinct sets, two of which must be put under *Robertianum* (see p. 325) and another (Ref. No. 4581) from the rocks west of Ballyvaghan, which is apparently a local form, since plants from the vicinity sent me this year by Mr. P. O'Kelly are not identical. Mine were small prostrate plants agreeing very closely in facies with Jordan's type *Villarsianum*, had

yellow anthers (therefore not *Robertianum*) and almost odourless foliage. The specimen I examined has glabrous carpels, but I find in some others from Ballyvaghan a very few hairs are present. Jordan in constrasting *Villarsianum* with *Robertianum* does not mention the hairiness of the carpels, but he includes in his diagnosis " glabris," and his type specimen, which is young, at Kew, Mr. W. B. Turrill tells me has glabrous smooth carpels. But a point of interest arises. Is the hairy or glabrous character of the carpels adequate to separate the two groups ? I have plants indistinguishable from *Robertianum* by other characters, and from inland situations, with glabrous carpels, whereas many plants passed as *purpureum* by British authors have more or less hairy carpels. It may be borne in mind that Syme (Eng. Bot. ii., 204) says the hairs are deciduous, and the hairiness varies greatly in quantity. However the monographer of the genus in the *Pflanzenreich* has quoted Rouy and Foucaud's (Fl. Fr. iv. 95, 1897) arrangement, than which apparently he had nothing better to suggest. But it is quite evident that the last word has not been said upon the subject. Dr. Ostenfeld's suggestion that at any rate his Clare specimens may represent a special variety is extremely probable, and closer attention being given to the group may show that *Robertianum* has a parallel series of variations to *purpureum*, and that in Britain we may possess several endemic forms.

902. *Potentilla procumbens* Sibth. var. **subsericea** (Wolf in Mon. Potentil. 653, 1908, as forma), near Truro, I.P.E., 1911. I have also seen it near Penzance and from Dolgelly, Merioneth.

927. *Rosa sarmentacea* Woods var. *stenocarpa* (Déség.), Westwood, York. I.P.E.

942. *Rosa omissa* Déśegl. var. *submollis* (Ley), Silverdale, Lancashire, I.P.E., 1911, teste Wolley Dod.

1000b. *Parnassia palustris* L. (see p. 312). The dwarf plants with large flowers and fruits which we collected in the damp "slacks" of the Southport dunes, and which Dr. Graebner and myself thought formed a good variety, proved constant in the Berlin garden. Meanwhile it has been described and named var. *condensata* by Travis and Wheldon (Journ. Bot. (1912), 254) who have had the plant under observation for some years. This year I have also seen it on low cliffs at White Park Bay, Antrim, and in Forfarshire on the Sands of Barry.

1015. The new species of *Sedum* which Prof. Graebner proposes to name after the writer has been already alluded to ; it appears to replace *S. acre* in Britain so far as the native habitats are concerned.

1077. *Mesembryanthemum acinaciforme* L. Under this name Prof. Graebner (p. 176) alludes to the Cornish plant. I am hoping to get Dr. Schönland's opinion on it, as the plant was named *aequilaterale* by English botanists (see *Flora of Cornwall*), while I rather leant to its being *M. edule.*

1260. *Erigeron borealis* (Vierh.)=*E. alpinus* auct. Brit. To this name Ostenfeld (p. 120) refers the British *E. alpinus*, differing as it does from the true plant by the obtuse basal leaves, the rather sparingly hairy base of the stem, and the strongly hairy, often purple phyllaries, characters which would have led me rather to call it var. *borealis*, than a distinct species.

1401. *Senecio vulgaris* L. forma *crepiformis*. The Blakeney plant with conical receptacles, which I thought might be due to a fall, I find are really owing to the attack of a small larva.

1420. *Arctium nemorosum* Lej. This name as Dalla Torre and Sarntheim (*Fl. Tirol*, 595, 1912) show, must be replaced by that of *A. macrospermum* (Wallr.) Dalla Torre and Sarntheim.

1657. *Sonchus oleraceus* L. var. **albescens** Neum. Galway, Ostenfeld, see p. 120, a first British reference.

1695. *Erica Tetralix* L. A plant which was not uncommon at the Lizard plant with small corollas may be distinguished as f. **parviflora.**

1696. **E. Mackayi × Tetralix = × E. Praegeri** Ostenf. in *New Phyt.*, 120, 1912. This has been in cultivation in the Edinburgh Bot. Gardens for some time (although not I believe distinguished from *E. Mackayi*), the roots coming from Craigga More. There seem to be good reasons for accepting Dr. Ostenfeld's suggested name and origin of this plant.

1931. *Euphrasia stricta* Host. Dog's Bay, Galway.

1933. *E. brevipila* Burn. and Grem. Silverdale, Lancash.; Westmoreland; Dunkeld, E. Perth; Lawers, Mid-Perth; Trosachs, W. Perth; Ballyvaghan, Co. Clare; Killarney, Kerry; New Forest, S. Hants.

E. fennica Kihlm. This plant I collected some years ago on Exmoor, Somerset, but saw it again last year at Clifden, Co. Galway. Professor R. von Wettstein agrees to the determination, which was suggested by Professor Lindman. New to Britain.

1948. *Bartsia Odontites* Huds., var. *verna* (Reichb.) Dog's Bay, Co. Galway, I.P.E.

1960. *Melampyrum pratense* L. var. *hians* Druce in *Naturalist*, X, (1884-5), 35.

Dr. Ostenfeld (l.c. 123) suggests that this plant is a form of *M. vulgatum* Pers., but apart from the question of splitting *M. pratense* into two species, I srtongly demur to this well-marked plant being made a *forma*. If the differences justify two species being made out of *Erigeron alpinus*, surely the differences, not only floristic but of habitat, which exist between *hians* and the type, establish its claims at least to varietal distinction; indeed both Professors Schröter and Graebner thought it was a good sub-species. Through the kindness of the former botanist, who sent specimens to the well-known specialist on this group, Dr. Ronniger, the fact has been ascertained that he considers it to be identical with the sub-species *M. paradoxum* which he has described in Schinz and Keller *Fl. der Schweiz*, 489, 1909.

With regard to *M. vulgatum* Persoon, this was published in the *Synopsis*, ii, 151, 1807, as " 5. *vulgatum* (*pratense* L) flor secundis lateralibus, cor. clausis, cal. subcolorati laciniis adscendentibus, caul. ramosissimo. Engl. Bot. t. 113. *M. sylvaticum* Huds, Ray. Hab. in sylvaticis frequens. Cor. tubus albicans. Anth. subcoalitæ." Now it appears evident to me that this is a still-born name, being simply synonymous with *M. pratense*, which the author quotes. The next species is " 6. *alpestre* (*sylvaticum* L.)" where a similar unnecessary and invalid change has been made by Persoon. who adds "Obs. Ob nomina trivialia incongrua, hac duæ species ut plurimum com-

mutantur." From which it is evident that he changed the names not because they represented different species, but because they were not descriptive of their place of growth.

It may well be urged that there are two distinct races or species, one northern, the true *M. pratense*, and a second which has been called *M. vulgatum*; but to connect the species with Persoon's name, appears to be, if not invalid, at least undesirable. . . . *Hians* is a very unvarying plant so far as the deep golden colour of the corolla goes, but it has a small range of leaf-variation, and, therefore, if Persoon's name is admissible, it should be put as *M. vulgatum* var. (not forma) *hians*.

1899. *Mentha rubra* Sm. One of the mints collected in Cornwall in 1911 has been named by M. Briquet as var. **raripila** Briq. in Bull. Herb. Boiss iv, (1896), 782. The *M. rubra* from the side of the Tay, Perth, p. 318, Mr. C. E. Salmon (*Report Bot. Exchange Club* (1911, 113) would rather refer to *M. gentilis*, a not improbable suggestion; but until fresh material is obtained, I propose to leave it as it stands.

2075 *Lamium Galeobdolon* Crantz var. *montanum* (Pers.)= *Galeobdolon luteum* Huds. Ostenfeld (p. 23) remarks on this as the form found in Britain. I recognized this in the *Flora of Berks.*, 410,1897 ; the var. *vulgare* (Pers.). with quite another area of of distribution, *i.e.*, Sweden, Denmark, Germany, Austria, etc., has long leaf-like bracts, and has not yet been recorded as British.

2159. *Salicornia.*—The North Bull plant, found by Ostenfeld, Lindman and myself in 1911, is still under Dr. Moss' observation; he will probably name it as a distinct species.

2200. *Rumex obtusifolius* × *nemorosus*=*R. Dufftii* Hausskn. Cressbrook Dale, Derby ; Tay side, Perth, Ostenfeld, l.c.

2210. *Rumex Acetosella* L. var. *acetoselloides* (Bal.), Foulshaw Moss, N. Lancashire, Ostenfeld, l.c.

Var. *angiocarpus* (Murb.) Potter Heigham, Norfolk, and a form verging towards *acetoselloides*, Ostenfeld, l.c., Clifden, Galway.

2276. *Salix aurita* × *cinerea*=*S. lutescens* A. Kern. Some of the members of the Excursion thought one of the forms found near Clifden, Galway, was *S. livida*, but the Rev. E. F. Linton passes all my plants as the above, and Dr. B. Floderus has rejected the suggestion of *S. livida*, and believes these gatherings to be an *aurita* form, but is unable to see the presence of *cinerea*.

2315. *Helleborine palustris* (Schrank) (vel. *longifolia* R. and B.) var. *ericetorum* (A. and G.) Druce, Southport Dunes. Dr. Graebner assents to the correctness of my identification. It also occurs near Raven Point, Wexford.

2442 (2) *Juncus ranarius* Songen and Perrier (see page 321) : Southport, determined by Dr. Graebner. The claim to specific grade for this plant is challenged by Dr. Ostenfeld (p. 124) and he quotes Buchenau (*Mon. Junc.* in Engler's *Pflanzenreich*(1906) where he says " we do not find *J. ranarius* given as a species, not even as a variety. . . . We can no more give specific rank to the saline form of *J. bufonius* than we can make a separate species of a glabrate form of an ordinarily hairy species (*e.g.*, *Melandrium album*)." I am by no means anxious to get into the line of fire between two conflicting

authorities; but I think Dr. Ostenfeld is unaware of Buchenau's change of mind. When he wrote his monograph, it is true he did not think *ranarius* worthy of notice, but subsequently (as Dr. Graebner informs me), having seen its constancy in culture, he became convinced it was a good species. I may add that Dr. Ostenfeld's example does not appear to be well chosen, since we have a halophytic form of *Juncus compressus* raised to specific rank as *Juncus gerardi*, and this in less saline situations shows the passage to the type. Again in *Melandryum Preslii*, we have a purely glabrous form of *M. dioicum* (associated it is true with other characters), raised to specific rank. Moreover, *J. ranarius* does not appear to be strictly halophilous, since Dr. Graebner has named some plants, which I collected on sandy ground, in inland situations, at Pyrford, Surrey and Woolmer Forest, Hants., as *J. ranarius*; to which the suggested name var. *halophilus*, therefore seems quite inappropriate. Dr. Graebner tells me that when *J. bufonius* and *ranarius* grow together they can be readily distinguished.

2538.   *Scirpus cæspitosus* L. var. **austriacus.** (Palla). We are greatly indebted to Dr. Ostenfeld for his discrimination of two forms, and for his kindness in showing us how they can be identified.   I gathered *germanicus* in Co. Tyrone this year, and *austriacus* in Argyll and Inverness.

2684.   *Agrostis alba* L.   A common form with dark purplish-black florets was found at about 3,000 feet on Ben Lawers, but Professor Hackel does not separate it from the type.

2687.   *A. canina* L. var. *mutica* Gaud.   Killarney.

2733.   *Phragmites vulgaris* (Lam.) Druce (vel. *P. communis* Trin.=*Arundo Phragmites* L.) forma **latifolia.**   This large form with leaves, 4 cm. in breadth—much greater than those of the common reed—which occurred in the Broads, cannot, I think belong to the South European *Arundo isiaca*, since ours has deep-purplish panicles.   I overlooked mentioning it in my notes and am indebted to Dr. Ostenfeld for drawing attention to it: forma **cæspitosa** also occurs.

2745.   *Molinia caerulea* Moench.   Professor Hackel referred the plant from Crowden Clough (p. 322) with interrupted panicles to the type.

2761.   *Poa trivialis* L.   The form of this from Ben Lawers and from Crossfell, Cumberland, which Dr. Ostenfeld suggested might be var. **subalpina** Beck (Fl. Nied. Oster, 86, 1890), Professor Hackel does not separate from the type.

2827.   *Agropyron pungens*′(vel. *litorale*) × *repens*= × *A. Oliveri* mihi (p. 323) and l.c., (126, 1912), I am pleased Dr. Ostenfeld has independently come to the same conclusion respecting the Blakeney plants.   He suggests that *litorale* rather than *pungens* should be the name used.   Hackel, the well-known authority on the Gramineæ, still uses the name *A. pungens*, and to it he refers the Burlesden Bridge plant, which I thought was nearer *repens*.

2880.   *Asplenium.*   The remarkable form which appeared so intermediate between *marinum* and *Adiantum-nigrum* with which it grew, I submitted to our well-known fern specialist, Dr. Stansfield, who reported it to be only a form of the latter species.   Dr. Ostenfeld tells us that Christensen also refers it to the same plant.   This affords another instance of the fact that because a

plant has intermediate characters between two species, it need not necessarily be a hybrid.

2893. *Polystichum aculeatum* Roth. var. *lonchitioides* Deakin. Christensen puts this as *P. lobatum* var. *Plukenetii* (Lois) l.c. 127, but I am not certain which name has priority: they are, I take it, synonymous.

2923 (2). *Azolla filiculoides* Lam. We are indebted to Dr. Ostenfeld for determining the *Azolla* from Norfolk as this species, as I collected no specimens. This year, however, through the kindness of Mr. J. Cator, M.P., I have had specimens from Wood-bastwick, which prove the accuracy of Dr. Ostenfeld's determination. Our generous host, Mr. Beamish, also sent me specimens from the brackish waters near Queenstown Junction, which prove to be the same species (teste N. E. Brown) and additional to the Irish list. *A. caroliniana* Willd., however, occurs in the Cherwell, near Oxford and in the Thames near Sonning and Henley, as well as in the Pang, near Suleham, Berks.

As one practical outcome of the Excursion may be mentioned the acquisition of Blakeney Point with its interesting accumulation of shingle, which Professor Oliver has made the scene of his own patient and minute investigations, and which proved to our visitors an extremely fascinating area both for its ecological and floristic value. It therefore appeared to be most desirable that it should be preserved for all time as a nature-reserve, since besides the points of interests alluded to it, has a rich bird fauna and many interests for the entomologist, as well as much scenic charm. Fortunately, through the generosity of the Fishmongers' Company and some others interested in the matter, a sufficient sum of money was placed in my hands, and through the kind help of Professor Oliver and other persons the troublesome and lengthy negotiations for purchase were eventually successful. To the shingle bank has been added an additional area of " saltings." This makes the reserve more homogeneous, and brings the total area acquired to more than 1,000 acres. Under certain conditions, and with the appointment of special trustees, the property has now been handed over to the National Trust; an object lesson, which it is hoped will have its effect in securing many other spots of interest to the naturalist and preserving them, as far as possible, in their pristine condition for all time.

THE BRITISH ASSOCIATION AT DUNDEE.

THE meetings of Section K at Dundee must be considered as quite successful, for though few of the older botanists were present, yet there was a very large attendance of the younger generation. It cannot be said that the papers read were unusually exciting, but nevertheless, taken as a whole, the meeting was very pleasant and instructive. The joint discussions provided a good deal of interest, though as is unfortunately often the case with carefully organized discussions, the fruitfulness of the result was perhaps scarcely commensurate with the labour expended.

PRESIDENTIAL ADDRESS.

Professor Keeble, the President of the Section, delivered an address which combined entertainment with instruction in quite an unusual degree, and was full of happy figures and turns of expression. It is thus eminently "quotable," a characteristic shared by very few of the addresses of Sectional Presidents in this or any other year.

THE FAULTS AND MERITS OF THE MODERN BOTANIST.

The President's first main thesis was that the modern botanist is a specialist who is not " on speaking terms with the cultured general public "—a defect which is partly due to faults of education, though partly inevitable because " as science becomes more complex, its followers think more and more in symbols, and those who think in symbols are apt to write in shorthand." The faults of education are due to English University students being treated " not as youths, but as men of mature mind." "The professorial potter takes the clay as he finds it, and, no matter what its state, fires it forthwith..... Were the assumption on which he acts well-founded, the method might be justified. If our undergraduates were, as we assume they are, well found in general culture, trained already in scientific method, familiar with the language of our fathers, and apt also to read and speak and write some other tongue, then let us take them straightway and bake them in the oven of specialisation." But the thing is admittedly not so, largely, let a University teacher suggest, the fault—and the very grave fault —of our schools ; but according to Dr. Keeble because " as society grows older its young men grow younger."

Again, " we are prone to forget that the twin gifts of youth are enthusiasm and idleness. The former we encourage, but the latter, falling within the category of morals, we visit with our displeasure. There is, however, an idleness which is not laziness, but a resting period of the organism tired with the trouble of growing up." Also, we may add, an idleness which is often found, alternating with bursts of productive energy, in those who are grown up, but have not settled down into rigid intellectual grooves. And those freer though less persistently laborious spirits we can ill spare. " I could wish " continued Dr. Keeble, " that our English Universities understood intellectual liberty as well as German Universities understand it. We are apt to mind our sheep too much, and to overrate the virtue of docility."...." It is never too

late for a well-trained mind to master a new subject, but he who neglects the substance of education for the shadow of mere knowledge robs himself of half the pleasure of his work and of every chance of greatness." Admirable doctrine, which we heartily commend to teachers and students alike.

The President then went on to claim that we had, after all, some virtues in greater degree than our Victorian predecessors : " theirs the higher meed of culture; ours, perhaps, the greater perspicacity." And a sign of this contrast is that while Mendel lived among them, it remained for us to discover his work.

THE MENDELIAN METHOD AND THE PROBLEM OF FLOWER-COLOUR.

This served to introduce the second main topic of the address, the current applications of Mendel's laws. In the first place, Dr. Keeble claimed that " there can be no criticism " of the method of Mendelian research, because it is like a knife which can cut a loaf whose crust " has turned the edge of other implements." And then, after a short general exposition of Mendelian theory, he went on to consider the application of the Mendelian method to the analysis of flower-colour, with which his own researches have been lately concerned.

In the first place he called attention to the fact, which Mendelian research revealed some years ago, that two kinds of white flower have to be distinguished, the so-called " dominant " and the so-called " recessive whites." The first cross of a " recessive white " with a coloured flower gives a *coloured* F_1 generation and three coloured to one white in F_2. The first cross of a " dominant white " with a coloured flower gives, on the contrary, a *white* F_1 generation, and three white to one coloured in F_2. Of these three whites one " breeds true to whiteness," *i.e.*, is homozygous in respect of that character, while the other two are heterozygous, *i.e.*, when self fertilised, their offspring again show segregation, giving rise to three white and one coloured form ; and so on. This result is explained by the hypothesis that the dominant whites carry a factor for colour and also a factor for colour inhibition— an hypothesis which perfectly explains the observed genetic results and shews the fruitfulness of Mendelism by propounding " a series of questions to the physiologist and the biochemist."

After some illuminating remarks on the relation of the new method to the general—and hitherto quite insufficiently defined— problem of the variation of species, introduced by the observation that variation in the conditions of growth may alter the adult character in the case of the inheritance of an unpaired factor— the case cited being the destructive effect of heat on the colour inhibitor, leading to flushing of the flowers—Dr. Keeble went on to discuss the recent advances in our knowledge of the factors giving rise to plant pigments, and to show the very important results that are accruing from the combination of Mendelian and biochemical work.

" The merit of being the first to combine the genetical with the biochemical method belongs to Miss Wheldale, to whom, more- over, we owe a good working hypothesis of the nature of the

processes involved in pigment-formation." "Glucosides hydrolysed by emulsin yield chromogens, which, acted on by oxydases, give rise to anthocyan pigments." Miss Wheldale showed in 1909 that the chromogen and the oxydase were, in certain cases at least, inherited separately, and that their isolation or concurrence corresponded with the production of white and coloured flowers respectively. It is difficult to over-estimate the importance of this first demonstration of the actual material nature of the factors already recognised by Mendelian breeders.

Chodat and Bach put forward the hypothesis that " the complete oxydase consists of two parts—a peroxydase and an organic peroxide. An oxydase reacts with oxidisable reagents, such as guaiacum to produce a characteristically coloured product. Hence these reagents may be termed oxydase-reagents. Peroxydases react with oxydase reagents only if there be added, as a substitute for the organic peroxide of the complete oxydase, a source of active oxygen in the form of hydrogen peroxide. Both oxydases and peroxydases occur in the cells of plants, and may be identified in extracts therefrom."

The difficulty of using the results of the work of Chodat and Bach in carrying further the analysis of the Mendelian factors for flower colour on biochemical lines " lay in the unsatisfactory nature of the methods of identifying oxydases derived from plant-tissues." Keeble and Armstrong, by the use of α-napthol and benzidine, have now " been able to map out the distribution of oxydase and peroxydase in the flowers and other parts of various plants," and though " the technique is as yet imperfect," the results afford " strong confirmation, of the current hypothesis of the mode of formation of anthocyan pigments. This confirmation, however, was rendered possible only by the fact " that they worked " with races of plants bred on Mendelian lines, and hence of known genetic constitution."

Space does not permit us to follow Dr. Keeble any further into the details of this work, which is, indeed, considering the complexity of the phenomena to be investigated, only just begun. Nor can we do more than barely mention his concluding suggestion (based on the discovery that " after one or two days exposure to darkness, plants of *Primula sinensis* contain more peroxydase than sister-plants kept under normal conditions of illumination") to the effect that the numerous diurnal rhythms observed in plants may act through periodic fluctuation in the amount of oxydase present. But the methods employed are certainly taking us a step further into an understanding of the actual causes at work in determining the evolution of new races of plants, and, as is always the case when a union between hitherto distinct lines of investigation is successfully established, our knowledge is advancing, and is likely to advance in the immediate future, by leaps and bounds. We most heartily congratulate Dr. Keeble on a most stimulating and fascinating address, excellent alike in matter and manner.

The programme of papers was a full one. Portions of two mornings were devoted to joint meetings with other Sections, one with Section B (Chemistry), at which papers dealing with the biochemistry of flower pigmentation were read: the other with Section D (Zoology) was given to a discussion on " The Origin of Life."

Biochemical Papers.

Professor Armstrong gave a further account of his work on chemical variation in *Lotus corniculatus.* In some forms the action of chloroform vapour on the fresh plants indicates the presence of a glucoside by a change in colour. Plants from the South of England almost invariably showed the presence of the cyanophoric glucoside, while others collected in Ayrshire and also in Norway gave no reaction. Some plants give only a faint reaction, so that the glucoside may be regarded as latent; the intensity of the reaction has been, in the case of many plants, noticeably less this year. This suggests that the differences observed in the chemical constitution of the plants may be chiefly due to the conditions under which they have grown.

Dr. E. F. Armstrong gave an account of the work he has recently done in conjunction with Professor Keeble, on the chemistry of flower pigmentation. Anthocyan pigments in flowers are thought to be produced by the action of oxydases on chromogens, the latter being formed by the hydrolysation of glucosides. The oxydase can be regarded as consisting of two parts, a peroxydase and an organic peroxide, and in some flowers the peroxydase only may be present. Keeble and Armstrong have found that by the use of *a*-naphthol or benzidine the oxydases present in the flower can be localised, and further the presence of the peroxydase may be often be located. The former reagent is always confined to picking out the veins of the corolla, while the benzidine reaction is exhibited by the superficial cells.

The reagent shows that oxydases are produced when the flower petal is wounded, for example by pricking, but these are probably different from the pigment oxydases. When plants are kept in the dark an increase in the amount of oxydase is observed.

Mr. W. N. Jones read an interesting paper on the distribution of oxydases in white flowers. In these the absence of colour is presumed to be due either to the absence of one or both of the pigment producing bodies, *viz.*, chromogen and oxydase or peroxydase, or to the presence of an inhibitor checking the action of the oxydase or peroxydase. Investigation points to the existence of the following types of white flowers:—

(*a*). Those in which a chromogen or an oxydase both occur, but from some cause, such as their localisation in different cells, do not react together. On treating these with alcohol they go slightly brown, as they do when benzidine is used.

(*b*). Those containing chromogen and peroxydase, but requiring the addition of hydrogen peroxide to produce a reaction.

(*c*). Those containing a peroxydase but no chromogen body, these give a reaction only when benzidine is added together with hydrogen peroxide.

A chromogen can be extracted from the flowers of *Lychnis coronaria*, which may be used instead of benzidine in testing the last group of flowers.

Dr. Eyre read papers on the enzymes of *Linum* and on its variation with locality. The yellow flowers of Linaceæ contain no

glucose or enzyme, while the blue, white and red flowers contain more or less of these.

An interesting communication was contributed by Mr. LAWRENCE BALLS on "Thermotoxy or Factors in the Growth of Cotton in Egypt." He had previously shown that the temperature growth acceleration of a fungus hypha was arrested at a temperature of 37·5°C, owing to the formation and excretion of a toxic katabolite, and now brought forward evidence of a similar phenomenon in the higher plants. In Egyptian cotton under field conditions, growth takes place chiefly during the night, and, as a rule, follows the night temperature, but when the day temperature has exceeded 35°C the growth during the following night is subnormal, limited by the accumulated toxin. If a normal day follows the toxin is decomposed—probably oxidised, and the next night's growth is normal.

Different races and species of *Gossypium* differ in their liability to this poisoning, and there are indications that this liability is a character which shows Mendelian segregation. The growth-temperature curve of a root in non-aerated water-cultures suggests a similar toxic accumulation as the result of a limited air-supply.

Mr. W. E. HILEY contributed a paper on "The Values of Different Degrees of Centrifugal Force on Geotropic Stimuli." He described an ingenious apparatus based on the principal of Fitting's intermittent clinostat, by which seedlings in a box are submitted alternately to a stimulus of gravity in one direction and any pre-arranged centrifugal force up to 20g. in the opposite direction. When the two opposing stimuli neutralise each other and the radicles show no ultimate bend, it is found that the product of the stimulating force multiplied by the time of action is the same in each direction. But these results were only obtained when the times were short. If the sum of the individual times in the two directions is greater than fifteen minutes, the larger force has less effect than that calculated on the basis given, and the radicles must be exposed to the force for a longer time in proportion to the period of rest.

Professor BOTTOMLEY has found that when peat, which is acid in reaction and contains no soluble humates, is treated with certain micro-organisms, a large quantity of soluble humus is produced and the peat is rendered alkaline. An aqueous extract of the treated peat will supply all the plant food necessary for successful water cultures, while plants fail to grow in raw peat extract.

Mr. A. G. HARPER dealt with vitality and distribution of growth in defoliated Larch trees. The general effects of defoliation were reduction in radial growth increment, and reduction in the ratio of the autumn tracheids to the total breadth of the annual ring.

MORPHOLOGICAL AND PALÆOBOTANICAL PAPERS.

Professor BOWER contributed an interesting paper on " The Origin of Indusium in some Ferns." Starting from the " Pterid-type " with the marginal flap of the fertile leaf covering the sori, the more primitive types of *Blechnum* show only a slight thickening of the flap about the point of greater curvature. But in the more advanced types such as *Blechnum brasiliense* a very considerable foliar expansion occupies the same position. Here the " indusial " flap is morphologically the leaf margin and the expansion is a new formation. The next step is seen in *Woodwardia* and *Doodya*, where the elongated sorus of *Blechnum* is divided into rows of separate sori, but this " indusium " is still a marginal flap.

This origin of the indusium is distinct from that in other types of ferns, and it is possible now to distinguish at least five different phyletic origins of protective structures passing under the general name of indusium.

Professor BOTTOMLEY read a paper on " The Root-Nodules of the Podocarpeæ." They are present in all genera of this group and are arranged in two distinct rows along the sides of the roots. They are developed from the pericycle cells opposite the two proto-xylems and are evidently modified lateral roots which are arrested from normal development by the entrance of bacteria into the cortical cells, in the first instance through the root-hairs. The bacterial tissue of the nodule, which surrounds its central stele, remains active for one season only, after which most of the cells lose their contents and their walls become thickened by bars of cellulose. The following spring a new mass of bacterial tissue is formed from the pericycle, and the old cells are squeezed out to form an outer protective zone. The formation of new bacterial tissue each year is characteristic of all root nodules concerned with nitrogen fixation.

Professor D. ELLIS communicated an account of the structure and multiplication of *Cladothrix dichotoma*.

Mr. R. B. THOMSON contributed some evidence with regard to the relative age of the Abietineæ and the Araucarineæ. Two forms have been considered to indicate the great age of the Abietineæ, *Pityoxylon chasense* from the Permian and *P. conwentzianum* from the Carboniferous. Dr. Gothan has shown that the reputed age of the latter cannot be considered as authentic, and the former is now shown to possess no structural features which are Abietineous. There is now no known Abietinean form, either in or earlier than the Trias, where the first undisputed Araucarian, *Woodworthia*, makes its appearance. Evidence from that and later species does not fulfil the demands of the Abietinean theory of the ancestry of the Araurearineæ.

The structure of a new specimen of *Sutcliffia* was described by Dr. ETHEL DE FRAINE. The chief points in its structure were the presence of a great thickness of secondary wood round the steles and meristeles, which are further surrounded by anastomosing strands of wood and bast. The latter recall those in certain genera of Cycads, and the view was upheld that the origin of the Cycad-

aceæ is to be sought in a monostelic form such as *Sutcliffia*, rather than in the polystelic members of the Medulloseæ.

Mr. H. Hamshaw Thomas described *Marattiopsis anglica*, a new Jurassic member of the Marattiaceæ which further indicates the great antiquity of that group.

Dr. Agnes Arber contributed a brief account of a new type of *Lepidostrobus*, possessing large sterile processes within the sporangium.

Other Papers.

A most interesting communication was made by Dr. Ostenfeld of Copenhagen dealing with experiments on the origin of species in the genus *Hieracium*. This paper appears in full in the present issue of the New Phytologist.

Professor F. E. Weiss gave an account of his experiments in breeding *Geum intermedium*. This form can readily be obtained by crossing *Geum urbanum* with *Geum rivale* and exhibits a remarkable blending of the characters of these plants. Its colour, for example, is due to the possession of both the epidermal anthocyanin of *G. rivale* and the yellow plastids of *G. urbanum*. The hybrid is perfectly fertile and both F_2 and F_3 generations have been raised. The F_1 generation does not vary very much, but in the F_2 generation the segregation of a number of important characters takes place, *e.g.*, the curvature of the peduncle, the presence of anthocyanin, the form of the calyx and petals. In the discussion it was pointed out that Professor Weiss's observations probably indicated the type of variation which had led to the appearance of the existing forms of the allied genus *Rubus*, while on the other hand Dr. Ostenfeld had indicated that the polymorphism of the Hieracia was due to entirely different causes.

Miss M. C. Rayner gave an account of her work on the ecology of *Calluna vulgaris*, in which the results of some experimental cultures, undertaken in order to throw light on the soil-preferences of this plant, were indicated. In water cultures the seedlings grow equally well in neutral or faintly acid solutions, but are very sensitive to changes in the concentration of the culture fluids. In pot cultures with soil from the chalk-down outside the heather area growth is retarded and germination capacity is lowered ; bacterial colonies, often forming a sheath round the root-tip, are prominent on the roots of young seedlings. In sterile agar cultures, using extracts from the heather and chalk-down soils, unsterilised seeds show a growth of micro-organisms, chiefly mycelium with the former extract, and bacteria with the latter. The problem is then to discover if the peculiarities of *Calluna* are specific or if they depend on mycorhiza and the bacterial flora of the soil. Towards the solution of this question, it has been found that seedling roots are normally infected soon after germination by a mycorhizal fungus arising from the seed-coat. Seeds can however be sterilised and germinated on agar plates. Under such conditions germination takes takes place normally and the seedlings start growth in the usual way.

Mr. Macgregor Skene in dealing with the relation of Beech forest to edaphic factors, compared the English type on chalk with that growing at high altitudes in the Cevennes on schist free from

lime, and in view of their close similarity, expressed the opinion that they should be considered as parts of one plant-formation.

Dr. GATES in studying the somatic mitoses in the nucellus of *Œnothera lata* had observed cases in which reduction division appeared to be about to take place.

Professor D. H. CAMPBELL gave an account of some of the chief features in the vegetation of Venezuela and Guiana and the surrounding region.

The semi-popular lecture was given by Mr. I. H. Burkill on "The Botany of the Arbor Expedition : a study of the forests of the Arbor Hills, Eastern Himalaya."

EXCURSIONS.

Several successful excursions were made. On Saturday September 7th, a large party visited Tentsmuir and had an opportunity of seeing the interesting maritime vegetation which is so extensively developed there. On the same day a smaller party paid a visit to Glen Clova and spent a strenuous day seeing the alpine and sub-alpine vegetation and several of the floristic treasures of that classic ground. Other excursions were made to Loch Rescobie with its reed-swamps and fens, and to the maritime cliffs, north of Arbroath as far as Red Head. An excursion had been arranged for the opening day of the meeting, but was not very successful owing to the fact that few botanists had been informed about it. The idea of having an excursion on the opening day is a very good one if it can be previously advertised in some way, and it is hoped that in future this may be done. A. G. T.

H. H. T.

NOTE ON OIL-BODIES IN THE MESOPHYLL OF
THE CHERRY LAUREL LEAF.

IN the elementary class at the Cambridge Botany School the leaf of the Cherry Laurel, *Prunus Laurocerasus* L. is often used as a type for the study of leaf-anatomy. The following method is employed by the students. Sections of the fresh material are placed for a short time in methylated spirit and are then mounted and examined in dilute glycerine. In some preparations recently made in this way, it was noticed that the palisade cells contained green bodies of roughly spherical form, but larger than the chloroplasts themselves and of a more intense green colour. Moreover these bodies appeared structureless and highly refractive. On inspection they were found in every preparation, though unless the section were thin they were not at all conspicuous.

As there was some discussion concerning the nature of the bodies it was thought desirable to examine them more fully. For this purpose sections of the fresh material were cut and treated in various ways.

Sections mounted in water only, without previous immersion in alcohol showed the bodies, which now lacked the bright green colour, but were of a pale bluish-green tint. They had the appearance of oil drops or at least of drops of some highly refractive substance. It seemed then that the green colour noticed in the first preparations, was very probably due to the absorption of

chlorophyll by the drops. The short immersion in alcohol would serve to extract some of the chlorophyll from the chloroplasts, and the green colouring matter was taken up by the drops till they appeared bright green. Experiments were then made to test whether such an action would take place under these conditions.

An emulsion of oil and water was made and placed on a slide— that is small spherical bubbles of oil were present in a general medium of water. To this an alcoholic extract of chlorophyll was added, by running under the cover-slip. It was found that the oil drops took up most of the green colour, leaving the surrounding medium only slightly tinted.

The partition in a test-tube was also tried. As an example, cedar-wood oil was shaken up with some alcoholic chlorophyll extract and the whole allowed to stand and settle out. Most of the green colour went into the oil, leaving a pale green layer of alcohol floating upon the oil.

It was thought that sections known to contain oil might react in the manner. Sections of castor-oil seeds *(Ricinus)* were cut, left in water for some time to allow the oil drops to run together[1] and then stained with an alcoholic solution of chlorophyll. It was found in this case also that the spherical oil drops stained green and had then much the same appearance as the bodies in the leaf. It seems certain then that the green colour of the oil drops in the leaf, is due to the taking up of chlorophyll from an alcoholic solution.

As the chlorophyll fades from a section of the leaf treated with alcohol as described, the oil bodies become more conspicuous by contrast, as they keep their green colour for a longer time than the chloroplasts. In still older preparations the green colour disappears altogether from the chloroplasts and the oil drops become dark brown in colour, when they are even more conspicuous.

The oil drops or oil bodies are usually spherical in form, are slightly larger than the chloroplasts and fairly uniform in size. As a rule there is one only in each palisade cell, occupying a more or less central position. Sometimes there are two present. A few occur also in cells of the lower mesophyll and sometimes even in the lower epidermis.

In nature they are probably similar to the oil bodies described by Radlkofer, Monteverde and others and mentioned in Zimmermann's Microtechnique.[2] Monteverde[3] describes oil bodies, uniform in size, which occur singly in the mesophyll cells of the crystal-free Grasses. They also occur in the palisade and spongy mesophyll of the leaves of numerous other orders of plants. Monteverde considers that they are comparable with the oil bodies which occur in Liverworts.

Whether the bodies in the Cherry Laurel leaf are exactly similar to those mentioned is difficult to say, but their presence should certainly be noted in such a well known type-leaf as this.

[1] Strasburger & Hillhouse, Pract. Bot., 6th Ed., 1908, p. 33.

[2] Zimmermann, Bot. Microtechnique, Eng. Trans., 1893, p. 210.

[3] Monteverde, Bot. Centralbl. 43, 1890, p. 329.

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FLORAL EVOLUTION : WITH PARTICULAR REFERENCE TO THE SYMPETALOUS DICOTYLEDONS.

By H. F. Wernham.

IX.—Summary and Conclusion. Evolutionary Genealogy; and Some Principles of Classification.

WE have completed our review of the several sympetalous groups; and it may be well now to summarize briefly the facts to which reference has been made, and the conclusions which have been drawn therefrom.

We have from the outset, however, proceeded on the assumption that Sympetalæ have been derived from polypetalous ancestors, and we must examine the justification for this assumption before we proceed further.

The origin of the Angiosperms is one of the leading problems of systematic botany, and one of the farthest from solution. It is not improbable that the Dicotyledons and Monocotyledons have diverged from a common proangiospermous ancestry, neither being derived from the other (see fig. p. 385); but the question now before us is, whether the polypetalous and the sympetalous series of Dicotyledons stand in a similar mutual relation, or whether Sympetalæ have been derived directly from Polypetalæ in the continuous course of evolutionary descent.

Have Sympetalæ necessarily descended from polypetalous Dicotyledons ?

All the considerations which we have exhibited in the foregoing chapters point to the affirmative answer to this question with almost irresistible force. All the biological tendencies of floral evolution which we have traced are strongly suggestive of the phyletic continuity between polypetalous and sympetalous forms, and go to justify the name *Archichlamydeæ*, primitive perianths. The fusion

of separate petals to form a tube must be reckoned among the actual facts in the history of the flower; Sympetalæ have been derived from Polypetalæ.[1]

We will review briefly some of the arguments in favour of this conclusion. First and foremost is the close similarity, in respects other than the cohesion of the corolla-members, between various polypetalous and sympetalous groups—a similarity which has led to the suggestions made in these chapters in regard to the ancestry of many of the latter. Thus Ericales have been associated with a geranial ancestry, Primulales with a centrospermal ancestry, and so on. An extreme case of this similarity, so to express it, is the occurrence of polypetalous Sympetalæ and of sympetalous Polypetalæ—significant *excepta* which defy any sharp distinction between Archichlamydeæ and Sympetalæ. A polypetalous form like *Pyrola*, for instance, conforms in every essential detail with the flowers typical of Ericales, save only in its polypetalous character; while an extensive example of the converse—Cucurbitaceæ, a sympetalous family with unmistakeable and close affinity with an archichlamydeous group—has been exhibited in the preceding chapter.

Sympetalous forms occur with sufficient rarity among Archichlamydeæ to make the distinction between this group and Sympetalæ an extremely useful one to the practical systematist, however unnatural the separation may prove to be; but the wide area of the affinity over which sympetalous forms occur among Archichlamydeæ is somewhat striking, for most of the large orders are concerned, from the Ranales (*Hexalobus, Eupomatia, Cissampelos, Barclaya*), upwards. In some families of this series[2] we meet even with the paradox of sympetaly or a marked tendency to it, as a prevalent character of the family. Such is the case, for example, in Crassulaceæ (Rosales) in which the petals are usually united, at least at the base (*Crassula, Sempervivum, Tillæa*), and in some genera a definite corolla-tube is a constant feature (*Cotyledon, Kalanchæ*). Pittosporaceæ, another family of Rosales, exhibit a clear tendency to sympetaly, the union of the petals occurring in all stages of completeness, from merely basal cohesion to the formation of a tube. In Polygalaceæ the cohesion of some, usually three, of the petals is an essential feature of the curiously zygomorphic flower. The tribe Cuspariæ of Rutaceæ is characterized by the possession of a corolla-tube; *Correa*, of the same family, has been

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[1] Bentham and Hooker's name for Archichlamydeæ with two perianth-whorls.

[2] Apart from Cucurbitaceæ (*supra*).

referred to in Chapter II. Other archichlamydeous genera in which a corolla-tube occurs in all the species are *Gomphandra* (Olacaceæ), *Montia* (Portulacaceæ), *Lonchostoma* (Bruniaceæ), *Quassia* (Simarubaceæ), *Hedwigia* (Burseraceæ), *Chisocheton* (Meliaceæ), *Tapura* (Chailletiaceæ), *Antholoma* (Tiliaceæ), *Fouquiera* (Tamaricaceæ), *Carica* (Caricaceæ), *Axinandra* (Lythraceæ), *Brachystum* (Melastomaceæ) ; and the petals are united in many species of *Connarus* (Connaraceæ), *Loasa* (Loasaceæ), *Opuntia* (Cactaceæ), *Marlea* (Cornaceæ). Basal cohesion of the petals occurs more or less frequently among most if not all of the families referred to above, as also in Resedaceæ (*Oligomeris*), Droseraceæ (*Byblis*), Saxifragaceæ, section C of Sapindales,[1] Vitaceæ (*Leca*), Malvaceæ, Sterculiaceæ, and section A of Parietales (Guttiferales). Beside these are those quite numerous cases in which the petals cohere above to form a cap, a feature common in Vitaceæ, Caryocaraceæ, Marcgraviaceæ, and Myrtaceæ, as well as other isolated instances in which the petals are united throughout *except* at the base (e.g., *Stackhousia*). Many of these latter cases of sympetaly, however, have conceivably no relation or analogy to the fundamental sympetaly concerned with the formation of a corolla-tube in connection with insect-visits and the concealment of honey.

The foregoing list includes most of the families concerned, but by no means all the genera ; a sufficient number of these *excepta* has, however, been quoted to give some idea of the wide area of relationship over which they occur.

If Sympetalæ have been derived from polypetalous ancestors, then we must regard the foregoing *excepta* as having leaped to sympetaly in the course of descent without advancing in any other character beyond those of some well-defined archichlamydeous group, and without acquiring such a complex of characters as would justify their inclusion in any known sympetalous group. This is the position we have adopted in regard to Cucurbitaceæ. We now have to refer to those floral forms which have advanced as far as some definite sympetalous group in all characters save that of cohesion in the corolla, the latter having lagged behind the other organs in the history of the flower ; these have necessarily to be included in Sympetalæ in spite of their polypetalous corollas.

The group which is richest in these latter *excepta* is Pentacyclidæ (Heteromeræ) ; and this is precisely what is to be expected on the assumption that Sympetalæ are the descendants of polypetalous

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[1] E.g., *Ilex*, including the common Holly.

ancestors. For it is in this group that the Economy Principle is but little advanced upon the stage generally characteristic of Archichlamydeæ, in which the andrœcium consists typically of two or more whorls. As we have seen in Chapter III, the working of the Economy Principle, reflected in Pentacyclidæ, bridges the gulf between Archichlamydeæ and Sympetalæ. At least 80 polypetalous species are included in Ericales—*Pyrola, Clethra, Ledum, Monotropa,* etc. Of Primulales, Myrsinaceæ have over 60 species with polypetalous flowers (e.g., *Embelia*) ; Primulaceæ include only a few such, viz., *Apochoris* and some species of *Asterolinum* ; in Plumbaginaceae the majority of the species have flowers with petals quite free or barely united at the base (e.g., *Acantholimon, Statice, Armeria*). The same applies to Styracaceæ, notably to *Styrax,* with over 60 species, and to Symplocaceæ, with over 150 species.

Turning now to Tetracyclidæ : in the flowers of the oleaceous *Linociera, Forestiera,* and *Fraxinus,* the petals are at most but slightly coherent at the base, and are often quite free ; over 20% of the Oleaceæ have flowers with free or sub-free petals. In the allied Salvadoraceæ, with scarcely a dozen species, polypetaly is the rule rather than the exception. Beyond these examples polypetaly is extremely rare in Tetracyclidæ, being confined almost exclusively to less than a score of species of Campanulaceæ (*Cyphia, Nemacladus, Dialypetalum*). Indeed, in the case of this last-named family, in which splitting of the corolla-tube is a common feature (e.g., *Lobelia*), it is questionable whether the dialypetalous condition is invariably primitive ; and the same question may apply to others among these *excepta.*

In our preliminary examination of the history of floral evolution (Chapters I and II), we were led to elucidate two main biological principles of advance, namely, the Economy Tendency, and the compensatory Tendency to Adaptation for the reception of Insect-visitors. The reflection of the working and mutual interaction of these two principles as seen in a general review of the various floral forms goes far to support the idea of progressive continuity of the two series of Dicotyledons ; for had the Sympetalæ as a whole been separately evolved from Proangiosperms, we should expect not unreasonably to find all stages of the working of the Economy Principle reflected as extensively among sympetalous as among polypetalous forms. This, as we have seen already in Chapter II, we do not find ; for quite 80% of the Sympetalæ have

flowers with isomerous or oligomerous andrœcium. Indefiniteness in the latter is confined to a quite small group, the Ebenales ; while the ranalian type of flower, with indefiniteness in all the parts, elongated receptacle and apocarpous gynœcium does not occur among Sympetalæ. The Archichlamydeæ are considerably less advanced in regard to the Economy Principle than are the Sympetalæ ; and flowers with isomerous or oligomerous andrœcium coupled with a bicarpellary ovary are very rare indeed in the former series,[1] but very common in the latter.

Again, the absence of any distinction between the essential organs of Archichlamydeæ and Sympetalæ lends further weight to the probability that the two form a continuous series; we cannot say in any and every given case that a stamen or an ovary belongs necessarily to an archichlamydeous or a sympetalous flower.

With regard to the evidence of the fossil record, this latter is so scanty in the matter of flowering plants that it may be employed only with the strictest caution. The evidence is necessarily of a negative character; but, so far as it goes, it supports the view which we are endeavouring to maintain ; for the records of Archichlamydeæ are plentiful in strata geologically earlier than that containing the first remains of Sympetalæ that have been discovered so far. Significant in the same connection is the fact that the Sympetalæ with regular flowers are manifestly prior to the zygomorphic forms, according to the fossil record.

Lastly, and perhaps the most significantly, the primordia of the corolla in Sympetalæ, in so far as the facts of floral ontogeny have been investigated, are usually free in the inception of development; the corolla is rarely, if ever, laid down in a continuous ring. A glance through Payer's *Traité*, frequently quoted in these chapters, will reveal this fact. The corolla makes its appearance in the form of separate papillæ, which fuse at a very early stage.

We conclude, then, that Sympetalæ have been derived from polypetalous Dicotyledons; our examination of the several sympetalous groups has been conducted on this assumption, and has led to results which may not be altogether unreasonable.

We should, perhaps, mention that it is by no means impossible for a sympetalous group to have been derived directly from, say, a proangiospermous ancestry, without the intervention of a polypetalous stock. A tubular perianth-whorl need not, of *primâ facie*

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[1] Apart from the exceptionally-advanced Umbelliferæ, which are epigynous.

necessity, be the product of fusion in the course of descent.[1]   In the writer's opinion, however, this is scarcely probable in the case of any of the known Sympetalæ. Apart from the abstract considerations which have just now been urged against such a probability, most of the component groups of this series are, as we have endeavoured to point out in these chapters, so clearly linked with the Archichlamydeæ and with each other in one evolutionary whole, that very few, if any, are left as matter for speculation from such a standpoint. Perhaps the only seriously isolated group is Plantaginales; but the floral organs of these plants, although combined in a peculiar way, reveal no fundamental differences from the corresponding organs in Archichlamydeæ when considered separately.

*   *   *   *

General Summary of the Sympetalæ.

The accompanying diagram has been devised for the reader's convenience ; it represents a portion of the evolutionary tree of the Vegetable Kingdom, namely, that portion, or most of it, which includes the branchings from the type of flower characterized by an elongated floral axis, and by indefiniteness and absence of cohesion in all the parts : this we have termed the Rañalian Common Ancestor. Proceeding from this, under the domination chiefly of the Economy Principle, is a line of descent which breaks ultimately into the three main lines leading respectively to the Geranial Plexus (Discifloræ of Bentham and Hooker), the Centrospermal Group, and the Calycifloral Plexus.[2]   It is from these three groups that the existing Sympetalæ, according to our conclusions, have descended.

The caryophylline branch of the Centrospermal Group, after the acquisition of a heterochlamydeous perianth and a unilocular ovary, gave rise to the Primulales, Plumbaginaceæ corresponding to the uniovulate or chenopodial section of that branch.

The general Calycifloral Plexus is exemplified in Rosales and Parietales (of Engler), and both display the transition from perigyny to epigyny.   The Ebenales represent the sympetalous progeny of that section of Parietales in which the ovary is prevailingly superior (Guttiferales) ; and this progeny reflects the condition of indefiniteness in numbers of the floral organs which is so marked a feature

[1] The Gnetaceæ possibly afford evidence of this.

[2] It is open to question whether Centrospermæ are derived from a ranalian floral type, but this does not concern us here ; it is with their descendants that we have to deal, not their ancestry.

Labiatae   Acanthaceae   Compositae   Umbelliferae   Dipsacaceae

DIOVULATAE (LAMIALES) (Schizocarpic)

MULTIOVULATAE (PERSONALES) (Non - schizocarpic)

AGGRECATAE (DIPSACALES)

Transitional TUBIFLORAE (POLEMONIALES)

CAMPANULATAE

Dipsacalian Stock

PLANTAGINALES

JASMINALES

CUCURBITALES

RUBIALES

Campanal Stock

Apocynal Stock

Rubialian Stock

Umbellifloral Stock

PRIMULALES

ERICALES

VACCINIALES?? (see text)

EBENALES

GENERAL CALYCIFLORAL PLEXUS (Rosales — Parietales)

GERANIAL PLEXUS (Disciflorae)

Centrospermal Stock

PARIETALES A (Guttiferales)

RANALIAN COMMON ANCESTOR (Poo Aoo Goo)
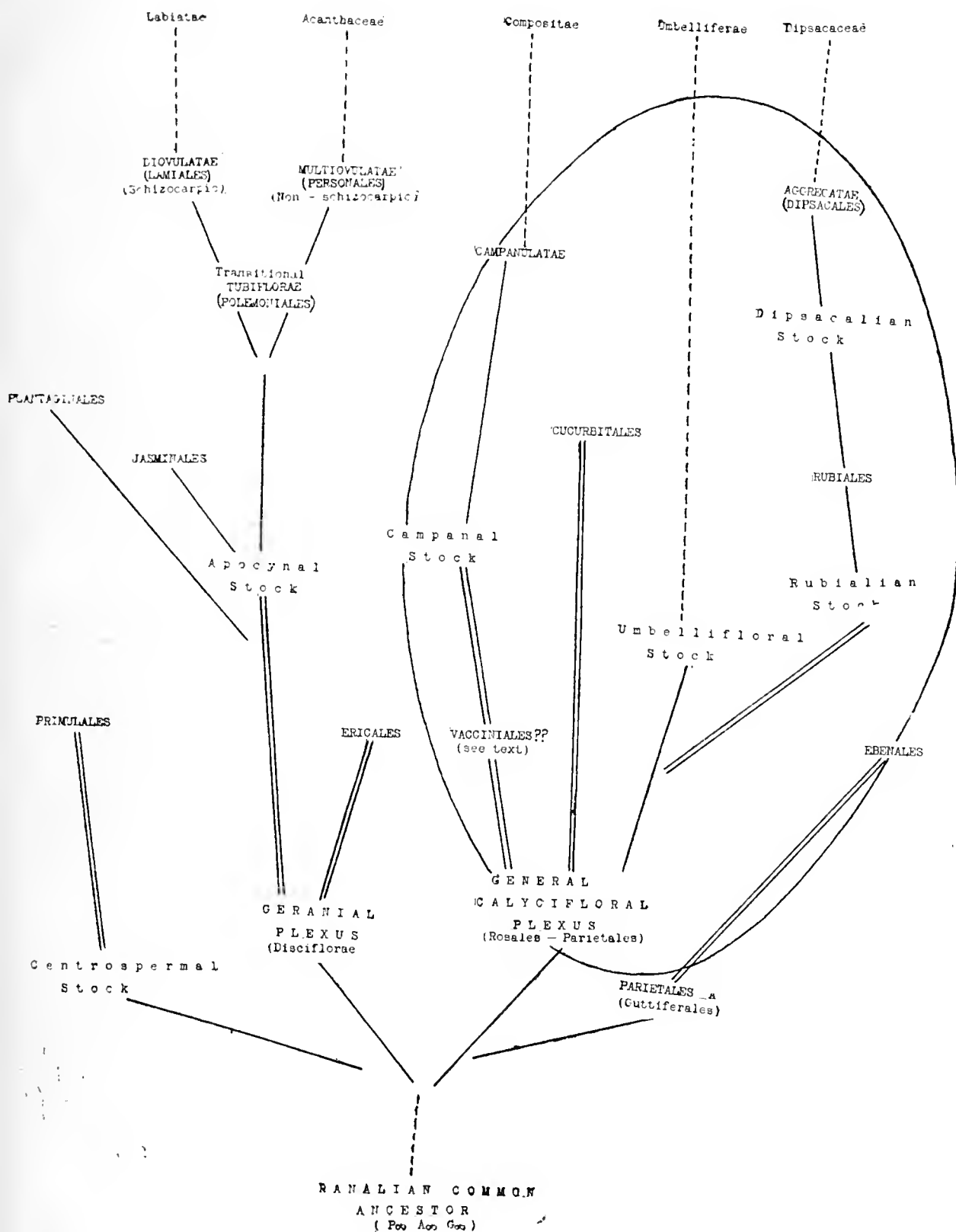
Diagram shewing the suggested heptaphyletic origin and the affinities of Sympetalæ. The seven double lines represent the progress to sympetaly. At the ends of the dotted lines, in the uppermost horizontal series, are the most advanced descendents of each group. The ellipse encloses all the epigynous forms, including most of the Campanal Stock and some of the Ebenales.

of Parietales generally. This section of Parietales is shewn in the diagram as emerging at an early stage from the calycifloral line.

From the Geranial Plexus two " sympetalous " lines diverge ; one of these led directly to Ericales. The three groups of Sympetalæ so far mentioned in this summary are peculiar in the character of an andrœcium of two or more whorls of stamens, or having the indication of two whorls by anteposition of the stamens to the corolla-segments (Primulales). They are thus intermediate between Archichlamydeæ and the majority of Sympetalæ (Tetra-cyclideæ), since they have made little or no general advance upon the former series in respect of the Economy Principle. For this reason they are grouped together in our modern systems, as Pentacyclidæ by Engler, and Heteromeræ by Bentham and Hooker. This grouping is, however, clearly unnatural, for we have seen that each of the three cohorts has a separate proximate archichlamydeous ancestry.

Primulales, Ericales, Ebenales, all have for the most part flowers with a superior ovary ; but the exceptions to this are important. The Primulales reflect the slight tendency to epigyny occurring in their caryophylline ancestry. In certain Ebenales appears the epigyny which is the main tendency of Parietales as a whole (see diagram, p. 379). But Ericales provide the most notable, exception, namely, the tribe Vaccinioideæ of Ericaceæ. These, unlike the rest of the Ericales, have epigynous flowers ; and we have raised the question (Chapters III and VIII) whether this tribe may not be descended from the calycifloral rather than from the hypogynous groups of Archichlamydeæ. In this case Vaccinioideæ would represent the Pentacyclidæ of the Calycifloral Plexus—otherwise unrepresented—and so would stand on the direct line to the Campanal Stock. The close resemblance and continuity, however, between Vaccinioideæ and the hypogynous Ericales in most of their essential characters makes an alternative view more acceptable, namely, that Vaccinioideæ represent a special line of epigyny emanating directly from Ericaceæ.

Each group of Pentacyclidæ represents the terminal point of a branch of the evolutionary tree ; where, then, is the line leading from Archichlamydeæ to the rest of the Sympetalæ with superior ovary ? For the answer to this question we have been led to postulate a second line emergent from the Geranial Plexus, the first being the ericalian line. There are, unfortunately, no pentacyclic forms to help us to cross this phyletic rubicon ; but once crossed,

the passage through Contortæ to Tubiflorae is relatively clear. We have surmised that the line now under consideration led to a hypothetical Apocynal Stock, in which the tendencies to an isomerous andrœcium and a bicarpellary ovary, already foreshadowed *separately* in Geraniales and Sapindales, are combined, being realized in the Contortæ. Of these we have separated Olcaccæ and Salvadoraceæ as representing a line determined by excessive working of the Economy Tendency in both mega- and micro-sporangia, naming the group Jasminales.

A third line emerging from the vicinity of the Apocynal Stock led, we suppose, to the reduced and specialized Plantaginales. This line is determined by the adoption of a particular and definite habit and by the aggregation of the small flowers into dense pedunculate spikes and heads. There seems to be no convincing evidence for the view that the Plantains are descended from any of the higher Tubiflorae.

The Apocynal Plexus gave rise directly to the Tubifloræ with isomerous andrœcium and regular flowers, our so-called Transitional Group, the Polemoniales of Bentham and Hooker. The connection is seen especially clear in Convolvulaceæ ; and the flowers of many of the higher Tubiflorae of various families recall their apocynal parents.

The fundamental distinction between the Transitional Group and the higher Tubiflorae lies in the zygomorphy of the corolla and consequent oligomery of the andrœcium in the flowers of the latter. The close connection between the two groups is seen in comparing Solanaceæ of the former group with Scrophulariaceæ of the latter. The tendency to zygomorphy and staminal oligomery is pronounced in Solanaceæ, and the Transitional Group is recalled in the sub-regular isostemonous flowers of *Verbascum*.

The zygomorphy of the higher Tubiflorae is held to be directly dependent upon insect-visits and so induced in the individual flower. It is thus independent of aggregation of florets into dense inflorescences which induces zygomorphy in the outer members. Two distinct " types " of zygomorphy are thus discernible, which we may name respectively the *Individual Type* and the *Aggregate Type*. Both types are illustrated in special and restricted circles of affinity throughout the Dicotyledons; but it is in the passage from the Transitional to the Higher Tubiflorae alone that Individual Zygomorphy has operated as the critical tendency of descent in the evolution of a large and varied existing group. Aggregate Zygomorphy,

we have seen, plays an important part among the descendants of the Calycifloral Plexus.

Within the Transitional Group an active fundamental differentiating tendency is reflected, namely, the progressive specialization of the fruit; this is exemplified particularly in Nolanaceæ and Boraginaceæ. The key-note of this specialization is "schizocarpy" —the association of a fruit-body with each separate seed, thereby extending the period of seed-protection without prejudicing seed-dispersal. This tendency, involving of necessity a considerable reduction in ovule-number, led to the section DIOVULATÆ of the Higher Tubifloræ—the LAMIALES of Bentham and Hooker.

Those Tubifloræ of the Transitional Group which escaped the tendency to schizocarpy retained an indefinite number of ovules in the ovary and led, in virtue of the acquisition of Individual Zygomorphy and consequent abortion of one or more of the stamens, to the MULTIOVULATÆ—the PERSONALES of Bentham and Hooker.

From the Calycifloral Plexus of Archichlamydeæ three distinct lines diverge. Two lead directly to sympetalous groups (CUCURBITALES[1] and the Campanal Stock), and the third indirectly (Umbellifloral and Rubialian Stocks). Of these the cucurbitaceous branch is to be regarded as quite short, in view of the close connection between Cucurbitaceæ and Parietales (Passiflorales).

Of the other two lines, the Campanal arose before the tendency to epigyny was fully realized, determined principally by the Pollen-Presentation tendency. The subsequent course of descent from the Campanal Stock (CAMPANULATÆ) is determined in the main by that aggregation-tendency which produced Compositæ, with its concomitant zygomorphy and reduction of megasporangia to one per floret. The side-shoot bearing Campanulaceæ and Goodeniaceæ appears at an early stage, determined by Individual Zygomorphy and progressive elaboration of the pollen-presentation mechanism.

The third line of Inferæ originated from the tendency to what we have called the " umbellifloral " arrangement of the flowers, in which the inflorescence is fundamentally cymose, and the flowers tend to lie in a continuous more or less expanded surface. This

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[1] A separate cohort (natural order) coterminous with the family Cucurbitaceæ. We conclude from our remarks on this group in the preceding chapter that its isolated position, relatively to the rest of the Sympetalæ, seems to warrant this rank. If, however, Cucurbitaceæ be retained among " Polypetalæ," it may reasonably be included in the same cohort with Passifloraceæ, as in the system of Bentham and Hooker ; and this latter most probably represents their true position in a natural scheme.

tendency is realized already in the descendants of the archichlamydeous Umbellifloral Stock (Umbelliflorae), represented by Araliaceae in which each ovary-chamber contains regularly but one ovule. From this stock the Umbelliferae arose as the expression of the bicarpellary condition of the ovary and of fruit-specialization, together with Aggregate Zygomorphy.

Before the evolution of the Umbellifloral Stock a sympetalous branch-line terminated in the Rubialian Stock. The existing representatives of this stock are the tropical Rubiaceae and the temperate Caprifoliaceae (RUBIALES), closely allied families differing chiefly in vegetative characters—possibly the result of the great and long-standing difference in habitat. In Caprifoliaceae, moreover, appear the beginnings of those tendencies which led to the sole progeny of the rubialian group, DIPSACALES ; namely, the tendency to Individual Zygomorphy coupled, as is usual, with oligomery in the androecium, and the tendency to reduction of the ovary to a, single fertile loculus. In Dipsacaceae, determined by a special tendency to aggregation, we may find both types of zygomorphy illustrated in the same inflorescence, and even in the same flower ; and the aggregation is accompanied, as in Compositae, Brunoniaceae, and other families characterized by heads of flowers, by reduction of the ovary to a single chamber occupied by a single ovule.

<div align="center">*   *   *   *</div>

The final conclusion of our investigations is that the Sympetalae are polyphyletic, in the sense that their origin cannot be traced to a single sympetalous ancestry. We have found, on the contrary, that the sympetalous Dicotyledons have descended from Archichlamydeae along seven distinct lines, *viz:*—

1. Centrospermae-PRIMULALES.
2. Geraniales-ERICALES.
3. Guttiferales-EBENALES.
4. Geraniales [PLANTAGINALES]. CONTORTÆ-TUBIFLORÆ.
5. Calyciflorae-Umbelliflorae-RUBIALES-DIPSACALES (AGGREGATE).
6. Calyciflorae-CAMPANULATÆ.
7. Calyciflorae-Passiflorales-CUCURBITALES.

We have adopted the names of actual groups—some borrowed from Bentham and Hooker as being more explicit; but the lines are to be conceived as traceable through hypothetical stocks rather than through existing groups.

Evolutionary Genealogy.

The terms "monophyletic" and "polyphyletic" are relative only; traced further down, our seven "sympetalous" lines converge upon the Ranalian Common Ancestor. Any polyphyletic group, in fact, is conceivable as monophyletic if its history be traced with sufficient remoteness. It is important that we should examine this statement in some detail.

Certain groups of considerable importance and extent have not made their appearance in our story of the Sympetalæ; such are the bulk of the Monochlamydeæ or Incompletæ of Bentham and Hooker. In this group these authors included those Dicotyledons in which the flower has only one perianth-whorl; and, to say the least of it at this juncture, the separation of Incompletæ from Polypetalæ seems to be as justifiable as the separation of Sympetalæ from Archichlamydeæ.

In an ideal system of classification, based, that is to say, entirely upon relationships, it may be that there should be no two- or three-fold division of the Dicotyledons. We have arrived at the conclusion that Sympetalæ, at any rate, should not exist as a separate group. If this be so, however, all the Dicotyledons must be referable to the branches of a single tree of affinities, with a single ancestor at its base. The latter must, moreover, be itself a Dicotyledon; otherwise the Dicotyledons will lie upon two or more separate trees connected in descent only at a point below, *i.e.*, preceding, the evolution of the Dicotyledons.

The accompanying diagram may serve to make this important point clearer. The ramifying lines represent that portion of the evolutionary tree upon which lie *all* the Angiosperms, ultimately descended, we suppose, from a pro-angiospermous ancestor A. The lines X, Y, Z, represent surfaces, the whole branch-system occupying all directions in space as may be necessary; X marks the boundary between pro-angiosperms and angiosperms, all the latter lying above it. Similarly all the existing and fossil Mono-cotyledons and Dicotyledons are supposed to lie above Y; so that the space between X and Y is occupied by Angiosperms prior in descent to the separation of Monocotyledons from Dicotyle-dons. Certain of the Ranales, *e.g.*, some of the Nymphæceæ, may not impossibly lie in this region. M and D represent the res-pective ancestors of the two groups, connected, we suppose, only through a pro-angiospermous ancestor A. The portion of the tree which we have investigated in these papers is enclosed in the circle

and all the Sympetalæ lie above the surface Z. Now we have called the Sympetalæ polyphyletic because the single ancestry, R, to which their evolutionary lines can all be traced does not itself lie above Z,—in other words, because they have not a single sympetalous ancestry.
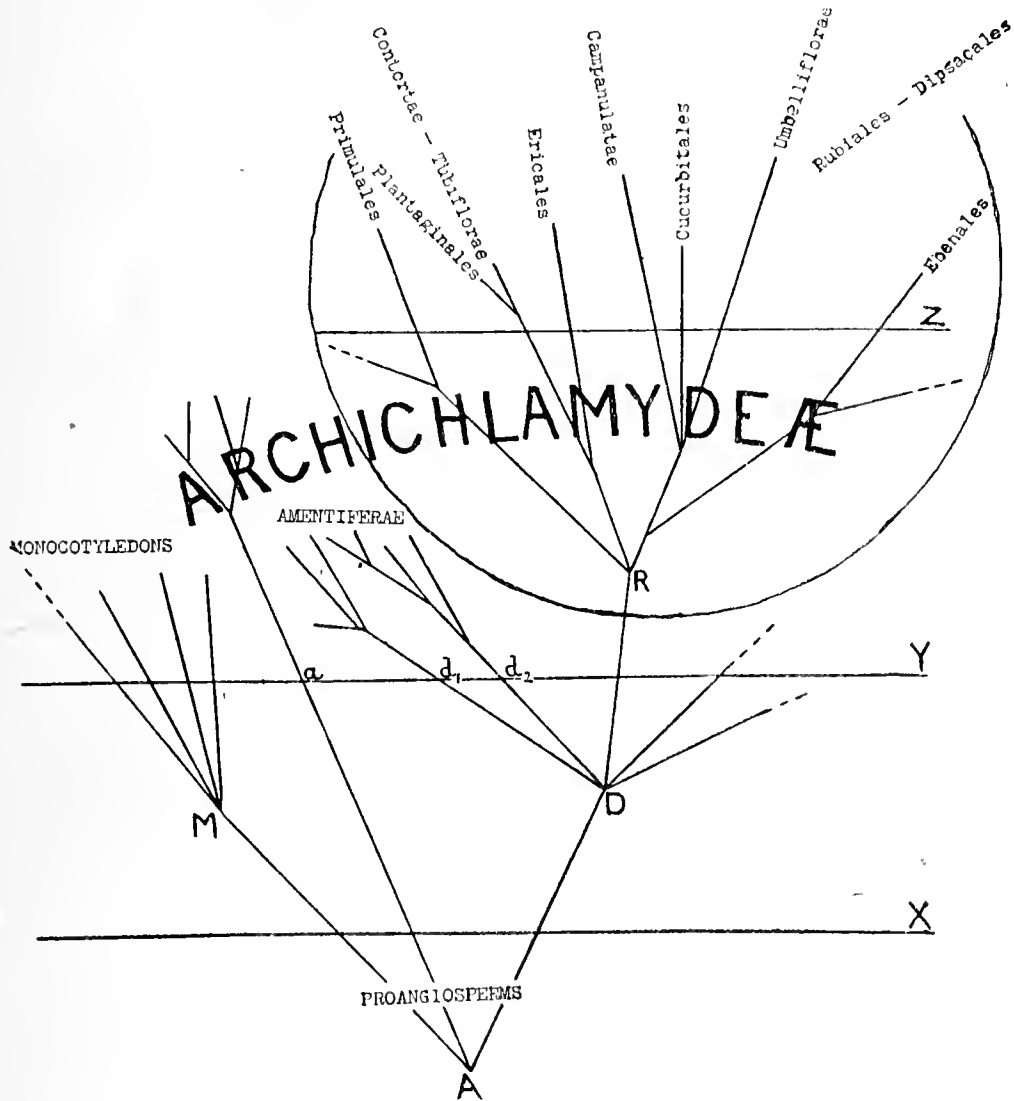
Diagram shewing possible lines of descent of the Angiospermæ from a proangiospermous ancestor, A. M, ancestor of the Monocotyledons, D, of the Dicotyledons. The Sympetalæ and their archichlamydeous ancestry are included in the circle, diverging from the Ranalian Common Ancestor, R. The lines are supposed to occupy all directions in space as may be necessary.

Similarly, both the Archichlamydeæ and the Monocotyledons may be, and probably are, polyphyletic in the same sense ; they are so represented in the diagram. Our present concern is with the former group. We have examined one evolutionary branch-system of the Dicotyledons, namely, that which has developed, under the several tendencies which we have attempted to trace, from an ancestor, R, of the ranalian type, with indefiniteness in all the floral parts, and an elongated floral axis. This explains our meaning when

we speak of this type as being relatively primitive. We have been led, moreover, to the conclusion that all the Sympetalæ lie upon this portion of the evolutionary tree.

But many of the Archichlamydeæ may not be referable to this portion. The biological tendencies which have been described in these chapters have in all probability operated in varying combinations, revealing themselves in many different ways ; other tendencies may have come into play, though such are necessarily limited in number ; the same biological advantage may be secured in more ways than one, as we have seen in the course of our studies. The net result has been that several lines of descent may have diverged from any particular stock D. Some of these lines may have persisted, the product of their determining tendencies being reflected in various groups, existing or extinct. Those which like DR persisted beyond the appearance of the Dicotyledons (*i.e.*, above the surface Y,—Dd_1, Dd_2 .... in the diagram) have, we suppose, in some cases at least, produced branch-systems of their own. It is upon one or more of such systems that many of the known Archichlamydeæ doubtless lie ; and far from being of necessity a single indivisible group, as the views of more than one modern systematist would seem to imply, the Archichlamydeæ must be separated into as many groups[1] as there are branch-systems of descent corresponding to the lines Dd_1, Dd_2 ... in the figure. The Archichlamydeæ are no less likely to be polyphyletic than are the Sympetalæ.

Engler's system has been justly applauded for its recognition of certain affinities which that of Bentham and Hooker does not express[2] on account of their maintenance of the group Incompletæ. But our approbation of the German system should not extend to its total abolition of this last-named group. Its superiority over the English system would have been indisputable indeed, had it banished the Sympetalæ and associated the component families of this series with their respective archichlamydeous predecessors in descent—Primulales with Centrospermæ, Ebenales and Cucurbitaceæ with Parietales, and so on. The group Incompletæ as it stands might indeed have been reduced in bulk ; places might be found for many of them among the progeny of the ranalian ancestor.

This supposed done, and all the dicotyledonous cross-affinities determined, would there remain no Archichlamydeæ whose con-

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[1] The Centrospermæ may come under this head.
[2] Notably the affinity of Caryophyllaceæ and their allies with the Curvembryeæ (Centrospermæ).

nection with our ranalian branch-system could only be traced through a pre-dicotyledonous, or even pro-angiospermous ancestor —the product of such lines as Dd_1, Dd_2, Aa, in the diagram ?

It is scarcely likely that all the known Archichlamydeæ have descended from a ranalian ancestor; although not a few represent in all probability the reduced and specialized progeny of familar groups of both Polypetalæ and Sympetalæ. Indications of the progress to " apetaly" are to be found in many typically hetero-chlamydeous families : one such case we have already noticed in connection with the Oleaceæ (*Fraxinus*); and there are many others, from among Ranales upwards.

We have found places for all the Sympetalæ in the branches of the evolutionary tree of the ranalian ancestry; but in an investi-gation based so largely upon mere speculation and so little upon actual fact the scope for error is great indeed. As we have insisted from time to time in these chapters, we cannot aspire to more than a few not unreasonable suggestions as to the general mode in which evolution has operated.

It is almost certain that some of the Archichlamydeæ at least have diverged from an ancestry other than the ranalian. Perhaps the most convincing evidence of this is afforded by the priority, in the fossil-record, of the catkin-bearing trees, the so-called Amentiferæ. In Permian and Triassic times coniferous trees probably stood in the van of the vegetable kingdom. Cycads appear in the Oolite, accompanied, perhaps, by screw-pines, grasses and other wind-pollinated monocotyledonous plants. Dicotyledons are extremely rare even in strata at the base of the Cretaceous system, in many cases deposited, like the Wealden, under the most favour-able conditions for the preservation of organic remains; and it is not until we reach the later Cretaceous beds that dicotyledonous plant-remains occur in any quantity. Our chief concern is with the fact that these earliest remains are prevailingly of amentiferous trees.

Their priority in the geological succession has been used as an argument to support the idea of the relative primitiveness of the Amentiferæ; and a similar argument has been applied even to the Monocotyledons.[1] The probable position of these groups in the history of descent will, it is hoped, be clear from our foregoing

[1] It is probable, however, that the first dicotyledonous fossil is as old geologically, if not older, than the first Monocotyledon (see Seward, *Notes on the Geological History of Monocotyledons*, Ann. Bot., X, 205).

remarks and from the diagram. Although we may compare the Monocotyledons and other groups with the ranalian progeny in respect of the mere order of their appearance in descent as reflected by the fossil-record, we cannot associate this comparison with conclusions of relative primitiveness. In other words, we may not say that a grass or a poplar is more primitive than a Magnolia, because the former precede the latter in the fossil-record ; for they lie on different branch-systems, which, diverged from a common ancestor before the separation of Dicotyledons and Monocotyledons ; they are incapable of comparison from this standpoint.

The crux of the matter is this, then, that if a form is referred · to as " relatively primitive," this statement must be treated as a strictly comparative one, and both sides of the comparison must be made clear; that is to say, the ancestor must be considered in relation to its progeny.

Many arguments have been adduced in favour of the primitiveness of certain amentiferous trees, but insufficient attention has been accorded to the nature and limits of the groups which are to be reckoned among their descendants. We have already, in our opening chapter, hinted at the probability that considerable reduction must have occurred in the course of descent to produce a solitary sporangium shared between two or more sporophylls —a common condition among Amentiferæ; we have, moreover, traced the history of a similar process in more cases than one—in the flower of Compositæ, for example. But we conclude that, in the case of the Amentiferæ in question, this reduction must have occurred at a remote period ; if, that is, they are to be regarded as " relatively primitive." They lie upon a branch-system different from the one which has been the subject of our examination ; they lie, therefore, outside our present province.

An important result of all this is that Incompletæ, called by that or some other name, reduced considerably, it may be, from its present proportions in the system of Bentham and Hooker, must, in contrast with Sympetalæ, be retained as a separate group in any natural scheme of classification; a group as isolated from the progeny of the ranalian ancestor as Mono-cotyledons from Dicotyledons; and, moreover, there may be several such groups; just so many, in fact, as there are lines of descent, Dd_1, Dd_2, ... persisting above Y and bearing existing or fossil forms upon their subsequent branches. Our ultimate conclusion, therefore, is that *the Sympetalæ should not exist as a*

separate group in a natural system of classification, however con-venient such a separation may be for practical purposes. They are capable of division into groups, each of which may be associated with a natural group of the so-called Archichlamydeæ. The Archi-chlamydeæ, on the other hand, fall into two or more distinct natural groups connected only through a relatively remote common ancestor—lying below the surface Y, we suppose, in the diagram, p. 385. This group as it stands in Engler's system is thus as unnatural as "Sympetalæ" has been shewn to be. We are, however, concerned only with those members which have direct connection with the existing sympetalous groups—and with them only in the most general way. The question of the origin and affinities of "Archichlamydeæ" involves the wider problem of the origin of Angiosperms, and both must form the subject of separate consideration, which is beyond our present scope.

<p style="text-align:center">*   *   *   *</p>

THE DETERMINATION OF PLANT-AFFINITIES. PRINCIPLES OF CLASSIFICATION.

The evolution of species, the outcome of the ever-present tendency in organisms to vary, is an accepted fact. This being so, plant-groups have a genealogical history, and all are connected in a scheme of relationship, of some such kind as we have just now sketched. Classification of plants in accordance with their relation-ships is the chief aim of the scientific systematist; and he is met at every turn by the practical difficulty of determining relationships; or, in other words, of ascertaining what the course of evolution has actually been. The difficulty is a very serious one, since observation is confined to internal evidence, afforded by the structure and habit of existing species and of a few fossil remains. Unlike the physio-logist, the systematist cannot experiment; he must base his conclusions upon the observation of achieved results, knowing little of the causes which produced them, and nothing of the course of their operation.

The problem before us is the elucidation of broad principles to guide us in the practical determination of affinities. Some such principles have necessarily been employed throughout the preceding chapters, implied if not expressed.

Our data are a number of flowering plants, each with its details of structure and habit, vegetative and reproductive—i.e., its *characters.* The problem reduces itself ultimately to this:—If a

number of plants have one or more characters in common, may we conclude therefore that they have derived those characters by descent from a common ancestry ? If so, then the plants should be grouped together, and we must determine further all the other plants which should be included in the same group, as well as the nature of the ancestry.

The ancestry is connected with its progeny in the evolutionary tree by a line; that line represents the changes induced in the ancestral characters by variation and transmitted to the progeny by inheritance. The fundamental point at issue is the nature of the characters which are to be deemed valid for the purposes just now enunciated—the *critical characters*. These determined, we have to seek for the ancestry, and discover in what way the ancestral characters have been modified to produce those of the progeny.

Constancy of Characters. Tendencies. We may gather from our previous investigations that the general relation between the significant features of the ancestry and those of the descendants is, that in the former the characters in question are not constant throughout the group, nor may they be completely evolved. In other words, we are dealing with *tendencies* to characters, and not with the critical characters themselves, in the case of the ancestry. In the progeny, on the other hand, the characters are constant and completely evolved; and the line which unites ancestor and descendants represents the transition between tendencies and their realisation. The descendants in their turn may reveal tendencies to other characters, to be realized in groups still more advanced.

It is in this connection that the significance of constancy and inconstancy of characters emerges; and it will be appreciated that a character may be of relatively rare occurrence within any group, and yet have considerable phyletic value, in so far as it throws light upon the evolutionary history of the group and its allies. Critical tendencies are no less important than critical characters.

Thus, the individual zygomorphy and androecial oligomery seen in a relative few of the Solanaceæ and Caprifoliaceæ are certainly not critical characters for the respective groups to which these families belong; but they are of great importance, since they reflect the tendency to characters which become constant and critical in Multiovulatæ and Dipsacales, the respective descendants of those groups. So also the umbellate inflorescence of Araliaceæ, representing the Umbellifloral stock, becomes, in the descendant Umbelliferæ, a very specialized biological floral-unit. Similarly, the

varying relative position of the ovary among the Calycifloraæ, variability which has brought epigyny into such sad disrepute as a classificatory character, is replaced by the constant epigyny of Rubiales, Cucurbitales, Compositæ, etc.

Inconstant characters which are phyletically important for a group as revealing its tendencies may have to be disregarded in sub-dividing that group. A good example of this is the oft-quoted one of the Rosales; for the same genus—e.g., *Saxifraga*—may include both hypogynous and epigynous forms; so that the relative position of the ovary, important as shewing the fundamental tendency of the Rosales, is often disregarded in the internal classification of this order.

We conclude, in any case, that characters which, by reason of their inconstancy in one group, must be disregarded for the purposes of classification, may become critical characters among the descendants of that group. Herein lies an explanation of the differing value of the same character in different circles of affinity ; and also an important modification of the principle that the critical value of a character is in direct proportion to its constancy.

Progress. By continuance of the process of uniting groups by lines of descent, we may endeavour to build up the evolutionary tree, and so construct a natural scheme of classification.

Now, if Variation and Natural Selection be actual and operative phenomena of the organic world, it follows that the course of evolution has been, speaking generally, in the direction of progress. But the question at once presents itself—What is involved in the idea of evolutionary progress ?

In view of the great difficulties and the host of side-issues which this question presents in its application to the Vegetable Kingdom at large, it will be well at the outset to confine our considerations to that branch of flowering plants which have formed the subject of our studies, namely, the Sympetalæ and their immediate ancestors. We may conclude from these studies that, limited to this field, at any rate, the idea of general progress involves, first, progressively greater efficiency for the business of the vital functions, coupled with, second, progressively diminishing " effort " or output to secure that efficiency.

The combination of these two factors is reflected in our two fundamental tendencies of Economy in production of reproductive parts and of Adaptation to Insect Visits. It is reflected also in the

tendency to the herbaceous habit which we have observed among the higher members of many series.

Many of the less advanced types may be as vitally efficient in their equipment as their descendants. In some cases, indeed, the ancestry may be more " successful " than the progeny ; and the latter may be, if not on the way to extinction, at any rate considerably restricted in numbers and distribution. This is the case with those examples of special complexity which, like Asclepiads, Candolleaceæ, etc., represent what we may term "experiments" of evolution, efforts attended by only partial or strictly limited success. Their very complexity militates against the wide-spread success of such forms. Such mechanisms, on the other hand, as occur in the floral parts of Compositæ, for example, entail a minimum of " effort " for their production. They are the direct result, in fact, of the mere growth and development of the floral parts ; yet they are at the same time eminently efficient for the performance of the vital functions of the production, protection and dispersal of the seed.

The simpler the structure, the more likely it will be to persist in the course of descent, so long as it is associated with a maximum of efficiency ; whence has resulted the pre-eminent success of the Campanulatæ-Compositæ branch of the evolutionary tree.

It is the evolution of this nice balance between simplicity of structure—economy in its widest sense—and efficiency of performance which constitutes " general progress "; and the principle of progress underlies all the general tendencies and determines all the *main* evolutionary lines.

"*Biological*" and "*Fortuitous*" *Characters.* Each line represents the progressive acquisition of some character or set of characters advantageous biologically. Progressive advance being the determining influence of the evolutionary story with which we are dealing, *biological characters*—i.e., such as are in direct relation to some vital function or advantage—cannot be neglected in any natural system of classification, however dangerous they may be in this connection.

For extreme caution must be employed in the use of biological characters in the determination of affinities. Plant-forms of widely-differing ancestry have undoubtedly tended to the acquisition of the same character of obvious advantage. To take an example from the many we have encountered in the course of our investigations, the aggregation of flowers into capitulate inflorescences is a character directly advantageous from the aspect of the biological

function of cross-pollination. It is therefore a biological character; and its occurrence in both Compositæ and Dipsacaceæ does not, we have seen, warrant the presumption that these are descended from a recent common stock. *A group of plants may share a number of biological characters in common without being therefore nearly related.*

Other examples of this important principle which will be familiar to the reader are afforded by the characters of sympetaly, zygomorphy, epigyny, etc. We have recognized the appearance of sympetaly in seven distinct and extensive circles of affinity; and attention has been called early in the present chapter to the occurrence of this character as the expression of extreme floral advance in many and diverse groups throughout the Archichlamydeæ. Its biological advantage is so great, so to speak, that cohesion of the petals is seldom neglected among the many evolutionary efforts to secure improvement in the floral mechanism. Similarly with zygo-morphy, epigyny, and other biological characters.

Again, it is clear that the vegetative characters of all the individuals in a peculiar and definite environment must within certain limits be in harmony therewith; hence it follows that all the individuals in that and similar environments may have certain vegetative characters in common, whatever their several ancestries may be. Such characters will yield no clue therefore to the ancestry. Whence, *Characters which are produced directly by the environment have no value in classification.*

If on the other hand two or more plants have a common character which has no relation to the environment nor to any biological function, we can only suppose this to be due to inheritance from a common ancestor. We know little of the cause of variation; but among the host of variations that arise in any given stock, some may be of little or no biological utility or significance. In so far as such variations are not positively detrimental to plant-life they will encounter no interference from the operation of Natural Selection, and so will conceivably be handed down by inheritance from one generation to another.[1] It will be convenient in the sequel to refer to variations and characters of this kind as *fortuitous.* The appearance of identical fortuitous characters in a number of plant-forms will thus create a reasonable presumption that they have

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[1] This view involves more or less the idea of descent by sudden mutations, and many may deny that useless characters have persisted through long lines of descent. In this case we shall be thrown entirely upon biological characters for phyletic purposes; this aspect of the matter is dealt with in the immediate sequel. In any case it will be remembered that biological characters have been our guide throughout our examination of the sympetalous groups.

derived them from a common ancestry. Examples of characters more or less fortuitous are provided by those often employed in systematic anatomy, *e.g.*, structure of stomata, nature of indumentum mode of deposition of mineral contents, and so on.

It may not be probable, nor is it impossible, that the same fortuitous character may appear as the result of mere coincidence in two plant-forms widely separated in descent. The multiplication of such characters, however, renders the possibility of coincidence negligible: whence, *The occurrence of several common fortuitous characters in a series of plant-forms is valid evidence of their mutual affinity; and the greater the number of common characters, the closer the affinity.*

The groups of lowest rank with which we have dealt in general has been the family.[1] In our modern systems the critical characters of the families are largely biological, and the same applies to the higher groups. It is scarcely surprising that the vital functions are reflected to a considerable if not predominating extent in the structures of the individual organism; and it is very doubtful if, even in a state of perfect acquaintance with all the details, sufficient purely fortuitous characters could be found upon which to base a natural classification.[2]

It is to the principle of fortuity in connection with biological characters that we must turn in the search for critical features; in other words, to the consideration that the same biological end may be attained in more than way. In the case of the Dipsacales we pointed out that the capitulum is the product of cymose branching, whereas the inflorescence of Compositæ is essentially racemose. This distinction led us to associate the former with the rubialian and the latter with the campanal stock. Zygomorphy, we have seen, has been produced in at least two ways, and epigyny in more than one. *In so far as a biological character may be acquired, or a vital function discharged, in several ways, then such a character is valid for phyletic purposes,* if it has been acquired within the circle of forms of which phyletic unity is predicated in only one of those ways; and its validity is greater or less in accordance with the number and definiteness of those ways. In so far as the number of ways is without limit, the biological character tends to become fortuitous as well. A looser, but perhaps simpler, way of expressing

[1] Formerly referred to as "natural order"—*e.g.*, Ericaceæ, Rubiaceæ, etc.

[2] See previous footnote No. 1.

the same idea is, that if a biological character be peculiar and well-defined, it may be of great value in determining relationships Examples of such characters are afforded by the pollen-mechanism of Asclepiads and Orchids, by the pollen-presentation device in Campanulatæ, and possibly by the mode of disposition of stereom in the plant-body. Indeed we may go so far as to say that the group Angiospermæ is founded not upon the biological character of a closed ovary, but upon the coincidence that the closed ovary is formed, presumably, in all the Angiosperms, in a particular way, namely by marginal fusion of sporophylls or rolling of a single sporophyll.[1] This excludes such forms as Bennettiteæ from the class of living Angiospermæ (see chapter I, p. 78 in Vol. X).

Group-Rank. The ideal system of classification is based solely upon the *history* of the various plant-forms. Groups of species have descended from a common stock representing the genus; groups of genera from a family-stock; and so on. The genus will comprise all the descendant species of the generic stock, no more and no less; the family, all the descendant genera of the family-stock. The genus, family, natural order, etc., are thus groups as "natural" as the species; but we cannot hope to attain more than the merest approximation to the complete display of these groups.

Vegetative and Reproductive Characters. The geographical distribution of a genus is, generally speaking, wider than that of a species, and the higher the rank of the group the more extensive its distribution. The characters of the higher groups must tend therefore to be such as are unaffected by particular environments, and their determinant tendencies such as make for increased efficiency irrespective of the environment. The vegetative characters, being concerned primarily with the life of the individual, are eminently susceptible—indirectly if not directly—to climatic and edaphic influences. The reproductive parts are virtually free from such influences; hence the most drastic changes in the environment may leave these parts unaffected in the course of descent.

It follows that, as regards biological characters, *the higher-ranked groups of flowering plants are determined by floral and not by vegetative characters.* Similarity in vegetative characters might be due to similarity in environment; whereas similarity in floral characters can only be due to their inheritance from a common

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[1] This is not necessarily the invariable rule; it is doubtful if the ovary of *Najas*, for example, is composed of sporophylls (See ch. I, p. 75, Vol. X).

ancestry : and it is only by the efficiency of the floral characters that inheritance is possible.[1]

The greatest biological need of the flowering-plant apart from its particular environment is the formation, protection, and efficient germination, of its seeds. This involves the functions of cross-pollination,[1] fruit-specialization, and fruit- and seed-dispersal. The part that these have played in the evolution of the Sympetalæ we have attempted to exhibit throughout our studies of each group. We have seen that the main lines of descent have been determined by two broad principles, economy and progressive efficiency for cross-pollination. Particular *stocks*, like the Apocynal, Campanal, Umbellifloral, and Rubialian, have been determined by the stage of advance attained in the course of particular tendencies on the lines of these principles ; and actual cohorts (natural orders) reflect the realization of those tendencies. Lines of inferior rank have been determined by fruit-specialization (Diovulatæ, Acanthaceæ, Umbelliferæ), by highly complex floral mechanisms (Asclepiadaceæ, Candolleaceæ), and even by peculiar and definite vegetative characters (Rubiaceæ, Lentibulariaceæ).

It is not to be wondered at if vegetative characters, necessarily so plastic, seldom constitute the basis of any very general tendency. We have noticed, however, that the most advanced members of particular evolutionary lines are prevailingly herbaceous ; and that, in the van of the flowering plant-class there is a general movement towards the herbaceous habit (Higher Tubifloræ; Campanulatæ; Dipsacales). This, we have seen, is explicable on biological grounds.

Natural plant-groups are often characterized by that complex of external features, chiefly vegetative, which constitutes the general *facies* or aspect. Such groups are exemplified in the tribe Ericoideæ of Ericaceæ, in Epacridaceæ, Cactaceæ, Gentianaceæ, Gramineæ, etc. This facies is often very distinctive, and, in combination with floral characters, affords valid evidence of descent from a common ancestry.

The interpetiolar stipules of Rubiaceæ provide, as we have seen, yet another example of the phyletic value of a purely vegetative character in relation to a wide circle of affinity. The climbing habit, again, characterizes certain extensive natural groups,— Cucurbitaceæ-Passiflorales, Convolvulaceæ, etc. In these cases it is not improbable that the vegetative character reflects a definite

[1] The assumption is here made that extensive groups of plant-races cannot persist either by asexual methods of reproduction or by self-pollination for indefinite periods.

tendency in the ancestry to respond to long-established climatic conditions, *e.g.*, the environment of the dense tropical forest.

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Within the space at our disposal we cannot aspire to completeness even in the most general examination of the principles of classification ; but the foregoing hints may serve to indicate a few of the modes of attack upon the all-absorbing questions of phylogeny, and to portray the relative value of the various kinds of characters. In the search after affinities it is all-important that no consideration should be left unnoticed before any conclusion is arrived at ; and too much stress cannot be laid upon that most obvious, most general, and yet so often-neglected principle that *Presumptions of affinity should not be based upon a single character ; the characters employed as criteria should be as numerous and as distinctive as possible ;* and biological evidence should be carefully examined in the light of the *history* in descent of the plant-forms under investigation.

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No more fit conclusion to these studies can, perhaps, be found than a special notice of the vast field for research which they have revealed at every turn. Surely, no branch of botany has suffered more through the lack of practical research than has the study of the Systematics of Flowering Plants ; and this by reason of the dearth of known facts of floral development in the great majority of the families of Angiosperms. And for the little knowledge that we do possess, we must needs turn for the most part to the work of more than half a century ago. Indeed, if we shall prove to have succeeded in stimulating ever so little the current of research in the direction in question, we shall feel that our labour has not been vain.
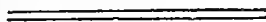
THE INTERNATIONAL PHYTOGEOGRAPHICAL
EXCURSION IN THE BRITISH ISLES.

XII.—Remarks on the Characters and Nomenclature of

some Critical Plants noticed on the Excursion.

By C. E. Moss.

*N*YMPHÆA *alba* var. *occidentalis* Ostenfeld in *New Phyt.* xi,
116 (1912). Mr. Druce still prefers the generic name *Castalia*
which involves the use of *Nymphæa* for *Nuphar;* but I do not
doubt that most botanists will be pleased to find that it is in strict
accordance with the international rules of nomenclature to retain
Nymphæa and *Nuphar* in their more familiar meanings (cf. Briquet,
Prodr. Fl. Cors., 577 (1911), and Rendle in *Journ. Bot.*, 277 (1911)).

It is interesting to note the two views which the members of
the excursion show a tendency to adopt with regard to this and
other new forms encountered on the excursion. On the one hand,
some members are inclined to regard them as characteristic of, and
related to, the insular climate of western Europe in general; and
this view is crystallised in the name which Dr. Ostenfeld has
bestowed upon the new water-lily. On the other hand, some other
members suggest more or less definitely that they are instances of
endemism in a continental island. It is too early to pronounce
any verdict on the merits of the two hypotheses; and indeed it may
well be that each will prove to be deserving of a measure of support.
I hope, however, that the theory of endemism will not be hastily
adopted, even as a working hypothesis. Before the new forms
receive new names, it is essential that they should be compared
with similar and closely allied plants known from the mainland of
Europe. This, of course, Dr. Ostenfeld has done; but it seems to
me there is a real danger in the theory of endemism as now being
put forward—a danger of new, or presumably new, British forms
receiving new names which will be found later to be mere synonyms
of older and well-known names in some Europæan countries. Even
if forms have arisen independently in the British Isles since the

Glacial Period, there are botanists who see no reason to forbid the belief that some such forms have since spread to the mainland.

Helianthemum chamæcistus Miller *Gard. Dict.*, ed. 8, no. 1 (1768). The tomentose form (*H. vulgare* var. *tomentosum* Irvine *Ill. Handb. Brit. Plants*, 690 (1858)) mentioned by Dr. Ostenfeld (p. 117 (1912)) is by far the commonest British form. The hairy form (*H. vulgare* var. *virescens* Irvine *loc. cit.*), however, does occur in England, as on a Greensand heath, in western Cambridgeshire. I have grown the two forms in my garden for three years; and the single separating character remains constant. I think that *Cistus surrejanus* L. *Sp. Pl.* 527 (1753), as figured in *Eng. Bot.* ed. 1, t. 2207, is the second of the above forms with an imperfectly developed corolla. *C. surrejanus* was discovered by Edward Du Bois in the neighbourhood of Croydon, Surrey; and Borrer used to find it occasionally in the same county.

Smith's *Cistus helianthemum* and *C. tomentosus* (=*Helianthemum tomentosum* Gray *Nat. Arr.* ii, 663 (1821)) refer to two forms of Irvine's var. *tomentosum*; but whether or not they are good varieties is doubtful. In any case, *H. tomentosum* Gray (*l. c.*) is simply *Cistus tomentosus*, Smith, *Eng. Bot.* t. 2208, which is founded on *C. tomentosus* Scopoli *Fl. Carn.* ed. 2, i, 376, t. 24 (1772). Both Smith's *C. helianthemum* and his *C. tomentosus* had leaves " densely downy, white, and hairy beneath." Hooker (*Brit. Fl.* 258 (1830)) thought *C. tomentosus* was not even a well-marked variety of *H. vulgare*, and reduced it to a synonym; and in this he has been followed by all British botanists. I should add that Smith's figure of his *C. tomentosus* has very differently shaped petals and leaves from that of Scopoli.

In the *Cambridge British Flora*, I propose to restrict the term sub-variety to forms like the above which are distinguished by a single but constant character, *i.e.*, a character which is, so far as one can judge, not directly caused by habitat-conditions, as seems to be the case with regard to the two forms of this species. To forms whose characters appear to be directly due to habitat-conditions (cf. *Polygonum amphibium* forma *terrestre*), I propose to restrict the term *forma*. Varieties will be those forms which are separated by more than one constant character, but which are not sufficiently far removed from their allies to be treated as species.

Stellaria dilleniana Moench *Enum. Pl. Hass.* 214, t. 6 (1777); *S. graminea* var. β L. *Sp. Pl.* 422 (1753); *S. palustris* Retzius *Fl. Scand.* ed. 2, 106 (1795); *S. glauca* Withering *Arr. Brit. Pl.* ed. 3,

420 (1796). There are several forms in England of this highly variable species in addition to the one noticed (p. 309 (1911)) by the party in Norfolk. Last year, in a fen in Huntingdonshire, I noticed that the following characters occurred in all their theoretical combinations:—(1) glaucousness (G); (2) non-glaucousness (g) or greenness; (3) large petals (P), about once-and-a-half to twice as long as the sepals; (4) small petals (p), about as long as the sepals, (5) many-flowered cymes (C); and (6) few-flowered cymes (c). All the forms grew in watery places in the fen; but, as regards their morphological characters, the " g p " forms were with difficulty distinguishable from the allied, and also variable *S. graminea.* In fact, by botanists of Bentham's school, such forms might be held to justify a return to the Linnæan view that *S. graminea* and *S. dilleniana* (=*S. palustris*=*S. glauca*) are simply forms of a single polymorphic species.

Now, many of the combinations of the above six characters have received names from systematists. Adopting, for the time being, the names in Rouy's *Fl. de France*, iii, 233 (1896), the following plants occurred in the fen in question:—G P=*S. palustris* var. *communis*; g P=*S. palustris* var. *communis* subvar. *viridis*; G p= *S. palustris* var. *parviflora*; g p=*S. palustris* var. *parviflora* subvar. *viridis*. Thus, if only the four characters, G, g, P, p, are considered, all the possible combinations are named. If, however, other combinations of two characters are considered, there are the following combinations unnamed:—G C, G c, g C, g c; and P C, p C, P c, p c.

There are also the following eight theoretical combinations to consider:—G P C, G P c, G p C, G p c, g P C, g P c, g p C, g p c. With regard to these, three of them have been named by Magnier in *Bull. Bot. Soc. France*, xxviii, 82 (1881); and G p C=*S. litigiosa* Magnier; g P C is *S. mœnchii* Magnier; and G P c is *S. heterophylla* Magnier. It will be seen that Magnier uses three characters, and names three combinations; but the following combinations he leaves without names:—G P C, G p c, g p C, g P c, and g p c.

The first form of the species to receive a binominal was g p c which was named *S. dilleniana* by Moench; and, as this name is valid, it must, by the rules of nomenclature, be used to designate the whole species. The later but more familiar names must unfortunately be discarded. Of these, *S. palustris*, like *S. dilleniana*, referred to a " g " form, as neither Linnæus nor Retzius mentions the glaucous character; and Withering's name *S. glauca* refers to

a "G P" form. The form figured in *Eng. Bot.* t. 825 is the "G P c" type. Mr. Druce recently (in *Brit. Bot. Rep. for 1910*, 546-7 (1911)) pointed out that the name *S. dilleniana* must replace the others.

It is obvious, I think, that the forms which have been named according to the methods of systematists have no stronger theoretical claim to be thus brought into prominence than those which have not been named. Ought we therefore to name the latter combinations, or reject the names of the former? To be logical, we should do either the one or the other.

I wish to ask, however, if it is not the case that the kind of variation which occurs in *S. dilleniana* is not amenable to the particular form of naming which systematists in all countries adopt? Is it not more desirable, in cases like this, where (so far as can be judged without experiments) characters hybridise and rehybridise and continue to be transmitted whole, to name the resulting forms by some symbolic method, such as is adopted by Mendelian workers? If this were done in systematic works, the combining characters would be indicated in the specific description, and the segregating forms would not be there named at all, except perhaps symbolically; and systematists need no longer, in these cases, encumber their works with an almost interminable number of sub-specific divisions and names.

To show how systematic works may be, and indeed often are, encumbered by names and synonyms of the forms here being discussed, let us consider the case of the characters G, g, P, p. Rouy (*loc. cit.*) divides these primarily by the characters of large petals (P) and small petals (p), thus having two varieties, P and p; then each variety is sub-divided by the character of glaucousness (G) and non-glaucousness (g), giving the sub-varieties G p and g p. But other botanists might first divide the species by some other corresponding pair of characters, *e.g.*, G and g, and sub-divide these by the remaining pairs; and this plan would result in sets of different names.

Again, who would say there are no additional characters to G, g, P, p, C, and c, say, for example, with regard to the width of the leaves, the width of the petals, the degree of splitting of the petals, and so on? Is each additional combination, as it is discovered, to receive a name?

If, in these and similar cases, the symbolical method of naming were adhered to, systematists would have fewer opportunities of becoming controversial in a vain attempt to settle which particular

one, of a number of equivalent biological forms, ought to be regarded as the "type" of the species.

The combination g P C named *S. mœnchii* by Magnier is not, as Magnier implies, the combination originally named *S. dilleniana* by Moench : this, as shown by Moench's description and figure, is g p c.

Sagina scotica Druce in *Rep. Bot. Exch. Club for 1911*, 14 (1912); in *New Phyt.* xi, 358 (1912); *S. procumbens* × *saginioides* Ostenfeld in *New Phyt.* xi.. 117 (1912). Roots of this critical plant, transplanted from Ben Lawers, have been grown in my garden. The plant spreads in the vegetative manner described by Dr. Ostenfeld. I do not, however, agree with Mr. Druce that its petals are " much longer " than the sepals: the petals and sepals are about of the same length ; and the description of the rhizome as " subligneous " is not very happy. The plant has produced seeds freely ; and these I have sown. It will be interesting to observe whether or not any of the characters show signs of segregation, as one would expect if, on Dr. Ostenfeld's supposition, the plant is a hybrid.

In connection with the suggestion of hybridity, I think that too much importance has been attached to the matter of seed-fertility. There are so many hybrids, even of species not very closely related (e.g., *Geum rivale* × *urbanum*) which are fertile, and not a few good species (e.g., *Ranunculus ficaria*) which are at least partially sterile in certain districts, that the matter of seed-fertility has really very little bearing on the question of hybridity.

Altogether there have been three suggestions as to the nature of the plant. I suggest that a fourth needs consideration. Is the plant a variety of *S. procumbens ?* If so, it is indeed a striking one; and, in any case, it is most curious that Scottish botanists have never named the plant before, though some of them allege that they have always been perfectly familiar with it. The view that the plant may be a variety of *S. procumbens* is suggested by the fact that it has a pronounced central rosette of leaves, as in this species.

Geranium robertianum L. Some discussion (p. 311 (1911) ; 118 (1912) ; 358 (1912)) has taken place regarding certain small-flowered plants allied to this species. I suggest that some (though probably not all) of these forms are hybrids of *G. robertianum* and *G. lucidum.* Last May, the British Vegetation Committee made an excursion in Leigh Woods, near Bristol. Here, growing between *G. robertianum* and *G. lucidum* was a small-flowered plant which is doubtless one of the varieties of *G. robertianum* "forma" [="race"] *purpureum*

Rouy *Fl. France*, iv, 96 (1897); but the position and the characters of the plant suggested that it might have had a hybrid origin. However, other of the forms in question may be good species or varieties, for it seems certain that forms may arise either as true varieties or by hybridisation, and yet closely resemble each other. As Professor Drude truly states (p. 237 (1912)), "the complexity of the subject has naturally been increased by new phylogenetic and ecological studies"; and this complexity seems more likely to be increased than diminished as time goes on. There is certainly need here, as in many similar cases, for experimental work.

Ulex Gallii Planchon *Ann. Sci. Nat.* ser. 3, xi, 207, t. 9 (1849). It will come as a shock to British botanists to know that this plant is, in Ascherson and Graebner's *Syn.* vi, pt. ii, 288 (1907), reduced to a hybrid of *U. europæus* and *U. nanus* (or *U. minor*). Of course, the distribution in this country of our three species of *Ulex* is wholly against such a view; and I am sure that no British botanist will agree with or sympathise with the hypothesis of the hybrid-nature of *U. gallii*. Rouy et Foucaud (*Fl. France*, iv, 243 (1897) also definitely reject the theory that *U. gallii* is a hybrid. As the plant is confined to France and the British Isles, the deliberate and unanimous verdict of French and British botanists should surely be accepted. However the plant was seen in many places on the excursion, so that the members had an opportunity of arriving at an independent conclusion.

I may add that *U. europæus* occurs throughout Great Britain, usually at altitudes below about 250 metres; that *U. gallii* gets no further north than southern Scotland, and usually ascends 100-200 metres higher than *U. europæus*; and that *U. nanus* is decidedly rare and local north of the Thames valley, has its northern limit in central England, and is a more pronounced lowland species than even *U. europæus*. In Ireland, both *U. europæus* and *U. gallii* are widespread and locally abundant; and *U. gallii* usually occupies a higher zone than *U. europæus*, *U. nanus* is unknown in Ireland. It will be seen that the distribution of the three species gives no support whatever to the view that *U. gallii* is a hybrid.

Pyrus aucuparia L. [*Pyrus aucuparia* "var. (or forma)" *flava* Druce in *New Phyt.* x, 312 (1911) nomen; *Sorbus aucuparia* var. *flava* Ostenfeld *op. cit.* xi, 120 (1912) nomen.] Pale-fruited forms are very interesting from the standpoint of the study of evolutionary variation; but it is a question whether they, and also the colour-variations in petals, should receive formal systematic names.

Parnassia palustris var. *condensata* Travis and Wheldon in *Journ. Bot.*, 254 (1912). This is the form seen in the damp dunc-hollows near Southport. I do not think this is an endemic variety. I have seen what I believe to be the same form in similar situations in Brittany; and I understand from Dr. Ostenfeld that it occurs in Denmark. Mr. J. Cosmo Melvill (*Journ. Bot.* l, 376 (1912)) contends that its characters are unstable, and that it should be reduced to a *forma*. Obviously, cultural experiments are indicated.

Sedum anglicum Hudson *Fl. Angl.* ed. 2, 196 (1778). Dr. Rübel informs me (*in litt.*) that the name *Sedum album* which appears in his charming account of the vegetation of Killarney (pp. 54-55 (1912) should be *S. anglicum*. Whether or not *S. album* is indigenous in the British Isles is doubtful.

Sedum acre L. (See pp. 356 and 359 (1912)). It may well be that the common form in this country differs from that in central Europe ; but it is, in my opinion, much too early even to hint at its being one of "quite a large number of forms endemic in Britain." Do Professor Graebner and Mr. Druce seriously maintain, at this early stage, that the new form does not occur, for example, in northern France ? However, until the plant has been described' one cannot state that one has seen it elsewhere, or that the common European form of the species is unknown in Great Britain and Ireland.

Œnanthe fluviatilis Coleman in *Ann. and Mag. Nat. Hist.* ser. 1, xiii, t. 3, 188 (1844); in *Eng. Bot. Suppl.* t. 2944 (1848); in Webb and Coleman *Fl. Hertford*, 369 (1849); Babington *Manual*, ed. 2, 141 (1847); Glück *Biol. und Morph.* iii, *Die Uferflora*, 429 (1911)); *Œ. phellandrium* var. *fluviatilis* Babington *Manual*, ed. 1, 131 (1843); [*Millefolium aquaticum* Dillen in Ray *Syn.* ed. 3, 216 (1728)]. Professor Drude (p. 238 (1912)) seems to regard this plant as of the same rank as the small varieties of *Helianthemum*, etc., which have been discussed in connection with this excursion; but that is not the view of those botanists who have carefully studied Coleman's plant. It may perhaps be arguable whether the plant is a species or a variety; but if it be reduced to a variety, it would be an uncommonly good variety, and consistency would demand the reduction of another hundred or more British species (exclusive of "species" of *Rubus*, *Hieracium*, *Euphrasia*, and the like) to varietal rank. In my opinion, the plant should remain as a species. Coleman studied it very carefully before naming it, and tested its constancy; his description is full and clear, and his figure accurate.

The species illustrates very well the danger involved in pushing to extremes the theory of endemism in British plants. The plant was ignored by continental botanists until quite recently, and was regarded as endemic by some British botanists.

Coleman when describing the plant gave his reasons for believing that the Œ. *phellandrium* of Koch was in part the new species; and Coleman's statement has received justification in Glück's discovery of Œ. *fluviatilis* in Germany and in Luxembourg. Further, Dr. Ostenfeld has this year found the plant in Denmark. The indications, therefore, are that, instead of being an endemic species, it will prove to be a member of the flora of other Europæan countries. I have no doubt that it will be found to occur in other parts of Germany—western Germany at least, in Holland, in Belgium, and in France; and I should not be surprised to find that it occurs in Switzerland and Austria. The determination of its northern, southern, and eastern limits will be an interesting question. Will it occur in northern Africa, like *Salicornia lignosa*, which was thought to be endemic in England up to two years ago? Dillen (*loc. cit.*), in the first British reference to the plant, cites " *M. aquaticum* Matth. *Ed. Valgr. in fol. P.* ii, p. 484; *aquaticum umbellatum coriandri folio* C. B. Pin, 141; *aquaticum foliis coriandii Matthioli*, J. B., iii, 2, 9." If these citations are correct, and they seem never to have been enquired into, there was no reason at any time for regarding Œ. *fluviatilis* as endemic in the British Isles.

The plant (Œ. *fluviatilis*) prefers running water: its ally (Œ. *aquatica*=Œ. *phellandrium*) prefers stagnant water. Its stem is fusiform and creeping at the base: that of Œ. *aquatica* remains cylindrical to the base. Its aërial leaves have broad, often almost overlapping, segments: the corresponding segments of Œ. *aquatica* are smaller, narrower, more acute, more deeply cut, and either not or scarcely overlapping. Its partial umbels have longer peduncles (*c.* 3 cm.) than Œ. *aquatica* (*c.* 1 cm.). Its fruits are longer (*c.* 5 mm.) than those of Œ. *aquatica* (*c.* 3 mm.), and are more compressed (*c.* 1 : 2) than in Œ. *aquatica* (*c.* 2 : 3). It is frequently a social plant, its stems and leaves often floating in an impenetrable tangled mass on the surface of small rivers and large drains, whilst Œ. *aquatica* in this country usually occurs here and there, in small ditches and in other stagnant waters. Both species vary considerably both as regards their respective land-forms and water-forms; and some of these have been named by Professor Glück. Each species may perhaps include a number of small locally endemic forms; but

Œ. fluviatilis is too distinct from its closest ally *Œ. aquatica* to be regarded as the kind of plant which would be endemic to the British Islands.

Arctium nemorosum Lejeune." The plant so named by many botanists was seen in many places on the excursion, as in Derbyshire, Lancashire, and Perthshire; but the name, as given above, has no claims to acceptance. It is merely a name—"*Arctium nemorosum* Lej. *in litt.*"—which appears in synonymy under *Lappa intermedia* Reichenbach *Icon.* xv, 54 (1853). Lange in *Dansk. Fl.* 357 (1886-88) cites " *A. nemorosum* Lej. *Fl. Spa* (1813)." However, I could find no such name in the copy of *Fl. Spa.* which I consulted; and Lange's omission of the page is suggestive.

Torre and Sarntheim (*Fl. Tirol* 595 (1912)) refer the plant to *Lappa macrosperma* Wallroth in *Linnæa* xiv, 639 (1840) ; but is this not *A. majus* Schkuhr *Handb.* iii, 49 (1808)? If this is so, the plant would appear to be better named *Arctium intermedium* Babington *loc. cit.* The Raian synonym, doubtfully cited by Wallroth, is referred to *A. majus* by Babington in *Ann. and Mag. Nat. Hist.* ser. 2, 372 (1856).

The plant is intermediate between *A. majus* and *A. minus* ; but it is not a hybrid, as its distribution in Great Britain (recently worked out by Mr. A. H. Evans, who will shortly publish his views on the British forms of *Arctium*) clearly shows.

Vaccinium oxycoccus var. **microcarpum ;** *Oxycoccus microcarpus* [Turczaminow in Sched. 1833, ex] Ruprecht *Hist. Stirp. Fl. Petrop.* 56 (1845).

As surmised by Professor Lindman, there are two forms of the cranberry in England, a small-fruited form and a larger-fruited one. I find that the former occurs on the peat-moors of the hills of the west and north of Great Britain, and I have recently collected it in Cheshire and Sutherlandshire. In addition to the size of the fruits, the large-fruited form is rarer and more local in the north; and it may be a lowland and southern form: I have gathered it in lowland moors in Somerset and Cheshire. The small-fruited form has glabrous pedicels, those of the large-fruited form being slightly hairy. In the small-fruited form, the flowers are 4-partite or commonly so, those of the large-fruited form being not infrequently 5-partite. The small-fruited form has rather smaller and more triangular leaves, and rather shorter petals. These are all minor differences, but the *ensemble* of characters is sufficient to constitute a variety.

As pointed out by Mr. J. Britten (*Journ. Bot.* viii, 291 (1870)) there are two fruit-forms of *V. oxycoccus*, one with spherical the other with pyriform fruits. I have seen pyriform fruits on the large-fruited form only, and near the Cheshire locality mentioned by Mr. Britten.

Gentiana nivalis L.—It is well known that the British form of this, gathered on Ben Lawers, is smaller than the alpine form. In addition to this, the Ben Lawers plant has rather broader leaves, and shorter and broader petals. In Swiss specimens, the petals are often less than half as broad as long; whereas in the Ben Lawers plant, they are about two thirds as broad as long. The Ben Lawers form here described is well depicted in *Eng. Bot.* ed. 1, t. 896.

It may be that the Scottish form is an instance of the local endemism of a small variety; but before it is named, I hope it will be ascertained whether or not it occurs abroad, and whether or not the Swiss form occurs in Scotland.

Lamium galeobdolon Crantz *Stirp. Austr.* ed. 2, 262 (1769); *Galeopsis galeobdolon* L. *Sp. Pl.* 580 (1753); Hudson *Fl. Angl.* 226 (1762); Miller *Gard. Dict.* ed. 8, no. 4 (1768); *Galeobdolon luteum* Hudson *Fl. Angl.* ed. 2, 258 (1778). Persoon (*Syn. Plant.* ii, 122 (1807)) briefly characterized two forms of this; and earlier names above cited would appear to be simple synonyms of *Galeopsis galeobdolon* L. Hudson's name, *Galeobdolon luteum*, is valid if the plant is removed from the genus *Lamium* into *Galeobdolon*; but I do not think it ought to be cited as referring to any particular segregate of the species. Persoon's first plant, his *Galeobdolon vulgare*, is briefly diagnosed by the words "fol. omnibus ovatis, involucro 4-phyllo," and Smith and Curtis are cited. The second plant, *G. vulgare* var. *montanum*, is summarised by the words "fol. summis lanceolatis, involucr. 6-8 phyllo." It is usually assumed that the British plants are the var. *montanum*, in spite of Persoon's allocation of synonyms; but British botanists (see Syme *Eng. Bot.* vii, 77 (1867) and Williams *Prodr. Fl. Brit.* i, 393 (1910)) have always assumed that the two plants were unworthy of recognition. This may have been because there is only one form in this country, as Dr. Ostenfeld suggests; but if so, the form is rather variable. It may be that further observation will reveal the existence of the second form also as a British plant. Syme (*loc. cit.*) adds that the English plant occasionally has " the bracts all broad and similar to the leaves (*G. luteum* Reichb.)." This remark applies to a plant drawn for the *Cambridge British Flora* by Mr. E. W. Hunnybun,

from the Isle of Wight; and this plant also has its leaves doubly serrate, the leaves of the barren stem strongly cordate, and the flowers more numerous in each verticillaster.

"*Polygonum aviculare* L." (agg.).—The forms of this excessively variable "species" were frequently discussed on the excursion. It was a great advantage to have Professor Lindman at hand, for he probably knows more about the forms in question than any other botanist. Quite recently, Professor Lindman (in *Svensk. Bot. Tidskrift*, vi, iii (1912)) has published his mature views with regard to them. He divides the aggregate "*P. aviculare* L." into two species, *P. heterophyllum* and *P. æquale*; and a third allied plant he had previously described as *P. calcatum*.

P. heterophyllum Lindman *op. cit.*, p. 690.—Common, chiefly in arable land, as far north as Forfarshire (!) at least.

P. heterophyllum var. **angustissimum** Lindman *op. cit.*, p. 691 ; *P. aviculare* var. *angustissimum* Meisner in DC. *Prodr.* xiv, 98 (1856).—This has been drawn for the *Cambridge British Flora* by Mr. Hunnybun, from Huntingdonshire specimens. Probably it is not uncommon.

P. heterophyllum subsp. **rurivagum** Lindman *loc. cit.*; *P. rurivagum* [Jordan ex] Boreau *Fl. Centr. France* ii, 560 (1857). This is very abundant in chalky cornfields, *e.g.*, in Cambridgeshire. It is usually described as an erect plant; but, like all forms of "*P. aviculare* L.," it is prostrate or decumbent at maturity. Almost every form of "*P. aviculare* L." has its small-leaved and small-fruited form ; and the latter are often named "*P. microspermum*."

P. heterophyllum var. **litorale** Lindman *loc. cit.*; *P. litorale* Persoon *Syn.* i, 439, 385 (1805) non Meisner.—This is a hemihalophytic form, the *P. aviculare* var. *litorale* of many botanists.

P. heterophyllum var. **cæspitosum** Lindman *loc. cit.*; *P. aviculare* var. *depressum* Meisner in DC. *Prodr.* xiv, 98 (18) partim. Recorded by Professor Lindman from near Cambridge.

P. æquale Lindman *op. cit.* p. 692. Common, as far north as Forfarshire (!) at least, chiefly by waysides.

Professor Lindman points out that the plants are visited by small Diptera, and suggests that hybrids occur. This suggestion is, in my view, a very reasonable one.

P. calcatum Lindman in *Botan. Notiser* 139 (1904).—Professor Lindman last year sent me specimens of this plant ; and I had no difficulty in recognising it, when I saw it on Arthur's Seat, near Edinburgh, last September. I sent a number of my specimens

to Professor Lindman ; and he replied:—"Your specimens are indeed *P. calcatum*, not the best I have seen, but *quite* safe." It grew near the roadside, among and almost hidden by the grass. It is best identified by its fruits, which are sub-bifacial with convex sides. It is a small, prostrate plant, nearer to *P. æquale* than to *P. heterophyllum*. It is an addition to the British flora.

Salicornia perennis var. **lignosa** comb. nov. ; *S. lignosa* Woods in *Bot. Gaz.* 31 (1851) ; Moss in *Journ. Bot.* xlix, 179 (1911).— After observing this plant for the last four years, I do not think it is sufficiently distinct from *S. perennis* (=*S. radicans*) to be allowed to retain specific rank. It is abundant on the western shore of Hayling Island, Hampshire, and was observed on the embankment there on the excursion on September 4th, 1911. I have seen it also in northern Algeria (near Oran), and in Brittany (the Bouche d'Erquy). It had previously been considered to be one of our endemic plants.

Salicornia dolichostachya sp. nov.—S. (dolichostachya) colore viridi v. flavo-viridi ; decumbens, flaccida v. subflaccida, sæpius ramosissima ; 5-30 cm. alta ; segmentis brevibus vel longis ; spicis longissimis (etiam 8-16 cm. longis), nonnunquam curvatis, brevibus sæpe ramis precipue ad basim, segmenta 15-30 exhibentibus. Differt ab omni alia specie annua quippe qua flores laterales inter se florem terminalem inclusum tenent perennium specierum ad instar.

In the accepted sub-divisions of the genus *Salicornia*, the distinction is made[1] that in the perennial species the lateral flowers are separated by the terminal one, whilst in the annual species the lateral flowers are not so separated : in the latter case, the central flower rests on the summits of the lateral flowers. *S. dolichostachya* is remarkable in being a bridging species in this regard, for, whilst it is an annual species, its lateral flowers are usually separated by the terminal one. That this is a very important character may be seen by observing the characters given in the definition of the sub-generic groups in all works where these are adopted. In addition to this character, *S. dolichostachya* may be recognised by its usually very " floppy " and decumbent habit, much branched, the branches tumbling over each other in a most disorderly way ; by its being the first species to come into flower (mid-August) and fruit (mid-September) ; and by its excessively long spikes, which are often

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[1] It may be pointed out that this character also needs revision with regard to the many-flowered forms, e.g., *Salicornia australis*.

curved, and often branched especially at or near the base.   I have had the plant under observation for three or four years.   It is very abundant and typical on the shingle near high-water mark on the western shore of Hayling Island, where it grows to the exclusion of the other annual species.   It was observed on the I.P.E. in Co. Dublin (*fide* Druce in *New Phyt.*, 318 (1911)) and on the northern shores of Hayling Island.   A small form of it occurs on the salt-marshes at Blakeney, Norfolk; and I have seen specimens from Essex (H. and G. Groves) and from Devonshire (*via* Rev. E. S. Marshall).   It also occurs in Spain (herb. C. Bailey) and Denmark (herb. Copenhagen).

The species of *Salicornia* are wind-pollinated; and hybrids are often abundant when allied species grow together.   *S. dolichostachya*, for example, seems to hybridise with *S. herbacea* (=*S. europæa*) when the two plants grow together.   I can only suppose the inter-mediate forms which occur in such places are hybrids, because they do not, according to my experience, occur when either species grows away from the other.   Similarly, hybrids of *S. her-bacea* and *S. ramosissima* occur, and doubtless of other species.

Salicornia dolichostachya X herbacea hybr. nov.—Hae plantæ medium locum tenent inter duas species a quibus nasci putantur, quibuscum etiam inveniuntur; colore viridi v. flavo-viridi; decumbens v. erecta, sæpius ramosissima, 5-20 cm. alta; segmentis longis (circiter 3-6 cm.), plus minusve erecta, interdum ramos habentibus eodem more quo *S. dolichostachya* segmenta circiter 8-20 exhibentibus; flores laterales aut includunt aut non includunt florem centralem.

This was collected on the excursion to Hayling Island, on the salt-marsh on the north of the Island, growing along with the putative parents.

Salicornia disarticulata Moss *op. cit.* p. 183, t. 514.   This also was observed in comparative abundance at Hayling Island.   It was interesting to hear the comments of the foreign botanists on this newly described plant which I regard as a good " Benthamian species."   One of them, with no leanings towards " Jordanian species," simply remarked :—" It is curious that such a plant has never been described before "!   It is abundant in several salt-marshes on the northern shores of Brittany, and in southern Great Britain, is known from South Wales to Norfolk.   It begins to flower, as a rule, on or about September 1st; and its disarticulating character—an

adaptation to seed-dispersal—may be observed during October and in early November.

Suæda maritima var. **macrocarpa** Moquin *Chenop. Monogr. Enum.* 128 (1840) ; *Chenopodium macrocarpum* Desvaux *Journ.* i, 48 (1813) ; *Suæda macrocarpa* Moquin in *Ann. Sci. Nat.* ser. i, xxiii, 309 (1831) ; *Chenopodina maritima* var. *macrocarpa* Moquin in *DC. Prodr.* xiii, 161 (1849).—This is the prevailing form of the species at Blakeney ; and it was also observed at Hayling Island. It occurs abundantly on the Bouche d'Erquy, and in other salt-marshes in northern Brittany. It flowers earlier than the small-fruited form, and has thicker, shorter, and blunter leaves. It is probably commoner in the British Isles than the small-fruited form which also occurred at Hayling Island.

Ulmus campestris L. Several foreign members of the party promised to look out for the English elm on their return to their respective countries ; but none has reported it. It is said to occur in Spain in certain of the royal parks.

I have elsewhere (in *Gard. Chron.*, March 30th, April 6th and April 13th (1912)), given my reasons for restricting the name *U. campestris* to the English elm. A later name is *U. procera* Salisbury *Prodr.* 391 (1796). The small (*c.* 1·25 cm. long) suborbicular fruits of the tree are very characteristic, as well as the long, straight, stout trunk, the widely spreading lower branches (often lopped), and the leaves which are always rough above as in *U. glabra* Hudson (=*U. montana*) and suborbicular on the lower parts of each young branch.

Salix repens var. *argentea* Duby *Bot. Gall.* i, 424 (1828) ; *S. argentea* Smith *Fl. Brit.* 1059 (1804); *Eng. Bot.* t. 1364 ; *Eng. Fl.* iv, 207 (1828). This form of *S. repens* is often a social plant on sand-dunes, as near Southport. MM. Camus *(Classif. Saul.* 168 (1904)) elevate the plant to a sub-species and Mons. Rouy *(Fl. France* xii, 209 (1910)) to a " race," but Rouy only confuses matters by changing its name to *dunensis*, and by retaining a var. *argentea* which is not Smith's plant. The charge of inconsistency suggested by MM. Camus and by Mons. Rouy against Sir J. E. Smith, to the effect that the latter confused his *S. argentea* in any way, cannot be sustained. In my opinion the var. *lanata*, A. et G. Camus (=var. *argentea* Rouy) is a silvery-leaved form of var. *fusca*, which forms the passage from var. *fusca* to var. *argentea*. Apart from its strongly social habit, I cannot see why var. *argentea* should be elevated to a higher rank than var. *fusca.* MM. Camus

and M. Rouy do not give any flower or fruit characters which definitely separate the two plants. *S. repens* var. *fusca* is the prevailing form of the species on the fens of eastern England.

S. aurita × *cinerea* Wimmer in *Flora* xxxi, 330 (1848). See p. 361 (1912). This is one of the commonest hybrid-willows of the British Isles. One never fails to find several forms of it whenever the two species grow together. It was observed on the Excursion in Wessenden Clough, near Huddersfield. On the alkaline fens of eastern England, *S. aurita* does not occur, except on the acidic " Hochmoor " patches and margins; and when *S. aurita* is absent and *S. cinerea* is present (as on Wicken Fen, near Cambridge), the intermediates or putative hybrids do not occur.

Orchis maculata L. This is another variable species whose forms, as a whole, have not been studied by British botanists, although certain isolated ones have been more or less carefully described. One form has been named, as "a sub-species or ... species," *O. ericetorum*, by the Rev. E. F. Linton. These alternative grades which are given to plants by their authors are very trouble-some to cite; and I think it is a good plan in all such cases to take the first suggested alternative as the one to be cited, and to ignore the second. This sub-species *ericetorum* Linton, then, is the form which was found in Crowden Clough, and is the usual British form on such siliceous and acidic soils. Mr. Druce maintains that it is the same as var. *præcox* Webster: if so, the varietal name chosen by this author is very inappropriate to the particular form which is abundant in northern England and in Scotland. A form of calcareous soils is var. *o'kelleyi* Druce, which was met with in Ireland, and which I have since found in a Cambridgeshire fen. It is one of the characteristics of fens, as opposed to moors, that they harbour a considerable number of calcicolous species. The common plant of England, on chalky or clayey soils seems to be the var. *trilobata* of Rouy's *Fl. de France* xii, 152—4 (1911). Perhaps we have other forms also; and certainly we have a considerable number of forms which seem to be hybrids of the var. *præcox* and var *trilobatus*, and hybrids of each of these with *O. latifolia* and *O. ericetorum.*

Juncus bufonius var. *ranarius; J. ranarius* Songeon et Perrier in Billot *Annot Fl. Fr. et d'All* 192 (1855). I confess to a good deal of sympathy with Dr. Ostenfeld in regarding this as being not specifically distinct from *J. bufonius.* The var. *ranarius* should possess outer perianth-segments which are equal to or

scarcely longer than the capsules, and inner segments shorter than the capsule. Similarly, I should prefer to regard *J. gerardi* as a variety of *J. compressus*, rather than a separate species.   In Ascherson and Graebner's *Fl. Nordostd. Flachl.* 175 (1898-9), *J. bufonius* and *J. ranarius* appear under the "Gesammtart" *J. bufonius.*

Zostera marina L.   Both the type and the narrow-leaved form were abundant near the bridge leading to Hayling.   The latter form is sometimes placed as a variety, sometimes as a hybrid of *Z. marina* and *Z. nana*; but all the narrow-leaved forms of *Z. marina* which I have seen *in situ* seem to be states related to habitat conditions.   It may be that a hybrid also occurs which simulates the narrow-leaved form of *Z. marina.*   *Z. nana* also occurred near Hayling Island : it seems to prefer less salty water than *Z. marina.*

Spartina townsendii H. and J. Groves in *Bot. Exch. Club Rep. for 1880*, 37 (1881) ; in *Journ. Bot.* xxi, t. 225 (1882) ; Stapf in *Gard. Chron.* ser. 3, xliii, 33 (1908).   The ecology of the *Spartinetum townsendii* of the Hampshire coasts is well deserving of an intensive study.   Personally, I do not regard it as occupying the place of any *Salicornietum* (cf. *of Brit. Veg. Types* p. 338) ; but as occupying a more outward or seaward zone.   The extremely flat ground, the exceptionally soft mud, and the comparative absence of a tidal scour are special features of this habitat.   At high tide, the *Spartinetum* resembles a reed-swamp of an open type.   All *Salicornieta*, often reclaimed on this coast, occur on the landward margin of the *Spartinetum* ; and a very extensive *Zosteretum marinæ* occurs on the sea-ward side of it.   The *Zosteretum*, also, is a special feature of this coast, and, so far at least as its large extent is concerned, is a unique feature among English plant-associations, though the *Zosteretum* is well-represented on the shores of some of the maritime lochs of north-eastern Scotland.

The points of general interest in the above notes are here summarised :—

1. Whilst it may be true that there are numerous endemic forms of plants in the British Isles slightly different from forms on the mainland of Europe, this hypothesis has no claims to acceptance until the British plants in question have been very carefully compared with the nearest related forms of the European mainland.

2. The naming of a new, or presumably new, sub-specific form collected in a particular locality is, in general, undesirable, unless at the same time the form in question is compared with other known forms of the species, and the distinguishing characters of these forms also carefully delineated.

3. In some cases (e.g., *Stellaria dilleniana*), the polymorphism of a species is of such a nature that is seems undesirable to name, other than symbolically, the sub-specific forms which are known to occur.

NOTES ON RECENT LITERATURE.

LIST OF BRITISH LICHENS.

A Hand-list of the Lichens of Great Britain, Ireland and the Channel Islands, compiled for the Lichen Exchange Club by the Secretary, A. R. Horwood. Dulau & Co., 1912.

MANY botanists who take an interest in the lichens of our islands have long felt the want of a list similar to that provided for flowering plants by the London Catalogue, and such a work has at length appeared, having been compiled from the British Museum Monograph[1] of these dual organisms. As the object of the list is to provide lichenologists with a ready means of indicating the contents of herbaria, marking for exchange purposes, and other similar uses, the compiler has made few alterations (except in the species of *Lecanora*) in the nomenclature adopted in the Monograph, but the classification adopted by Crombie has had to be widely departed from, the system followed being that outlined in a recent number of this Journal.[2] It is to be noted that the system adopted by Bruce Fink[3] and so lavishly and unduly praised by the compiler in the Lichen Exchange Report of 1910, has been entirely neglected. *Lecanora* has been rendered a less unwieldy

[1] British Lichens, Part I, by the Rev. J. M. Crombie, M.A., 1894. Part II, by Annie Lorrain Smith, F.L.S., 1911. Published by the British Museum.

[2] See NEW PHYTOLOGIST, Vol. XI, No. 3, March, 1912.

[3] The Lichens of Minnesota.

genus, being split up into twelve genera, according to the practice of some of the earlier lichenologists. The genus *Lecanora* as now understood only contains about 80 species instead of nearly 200. The splitting of this genus follows legitimate lines, being based primarily on the characters of the spores and apothecia and secondarily on the nature of the thallus. Some of these genera were given by Crombie as sub-genera, but his divisions were not altogether in accord with the practice of modern lichenology, and have not been closely followed in the list.

The division of *Collema* into three genera, *Lempholemma*, *Collema* (why *Eucollema* when it is not used in a sub-generic sense ?) and *Synechoblastus* is a legitimate one, since it is founded on definite differences in spore characters, but the adoption of Crombie's sub-generic divisions of *Leptogium* as generic names, should have been avoided, since these divisions hardly have a firm basis and should only be used sub-generically, if at all. *Polychidium muscicola* is rightly separated from the other *Leptogia*, since it has quite a different aspect from any other species of the genus, or indeed from any other member of the Collemaceæ. The authority for this name should have been Gray and not Fr.

In some other cases, it would have been better to have avoided raising sub-genera to generic rank : thus it seems unnecessary to elevate *Parmosticta* into a genus, when the only other British species of *Sticta* has very similar characters. For a similar reason *Agyrophora*, *Ionaspsis* and *Icmadophila* seem to be superfluities.

Physcia is unfortunately omitted from the list, all the species being included under *Xanthoria*, a correct name for *flavicans* and the four following "Physcias," with a yellow thallus and simple, colourless spores, but incapable of accommodating the other nineteen species (Nos. 249—267 in the list) with grey or brown thalli and 1-septate, dark-coloured spores.

The species of *Cladonia* are arranged almost exactly as they were by Crombie ; it is to be hoped that this genus will receive drastic treatment in the revised edition of the first part of the British Museum Monograph, the confusion and overlapping being almost as great as amongst the Lecideas and Lecanoras. *Cladonia luteo–alba* with red apothecia ought not to be included in the Phæocarpæ, and *C. Lamarkii* forma *Isigynii* is undoubtedly the same plant as *C. pityrea* forma *hololepis*, as far as one can judge by the descriptions and plants referred to them. *C. delicata* seems to be a form with the leaflets more or less granulato-leprose at the

margin, and probably includes derivatives of more than one species, whilst *C. cæspititia* is also a somewhat questionable species.

Amongst other minor matters it should be noted that *Ticho-spora* is not a true synonym of *Collemopsis* ; Stir should be Stiz. ; Scyphophoreæ and Ascyphæ (under *Cladonia*) should be definitely indicated as sub-divisions of Microphyllineæ ; Floerk. and Koerb. when so written (*i.e.*, with the e) do not require the " Umlaut " indicated by the two dots above the o ; and some of the authorities are wrongly given, *e.g.*, *Placodium candicans* should be referred to Mudd and not to Nyl. The compiler of the list has some strong, and I think warranted, views as to " the piracy of specific names," but in many instances he has neither adopted the method he agrees with, nor that followed by many authors of giving as authority the person who first placed the species in the genus. Mr. Macvicar in his recent and excellent work on the Hepaticæ[1] has followed the method of giving the original author of the specific name in brackets, followed by the name of the authority for the actual combination of the generic and specific names ; this method has been used by many authors, has the advantage of indicating the history of the naming, and avoids any charges of piracy.

Notwithstanding the necessarily incomplete character of the work, the List will provide British Lichenologists with a ready means of reference, and thus fill up a gap which has long been felt by students and collectors of these interesting organisms.

[1] S. Macvicar. A Handbook of British Hepaticæ, 1912.

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